PALEOBIOLOGY, BIOGEOGRAPHY, AND SYSTEMATICS OF THE BLACK-FOOTED FERRET, *MUSTELA NIGRIPES* (AUDUBON AND BACHMAN), 1851

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ABSTRACT.—Extensive literature review and 48 mammal collections containing recent specimens of the endangered black-footed ferret (*Mustela nigripes*) are used to characterize historic distribution of the species. Specimens (n = 120) were measured from eight collections to characterize black-footed ferret morphology and variation. Twenty-one Pleistocene and Holocene faunas in North America show ferrets dating to 100,000 yr B.P. Recent specimens (n = 412) indicate close association with the prairie dog (*Cynomys spp.*) and suggest ferrets may have been less rare than previously thought. At least 103 (25%) of all specimens were taken by federal predator and rodent control agents, and males outnumber females in collections 2.04:1. Average and extreme measurement for external, cranial, and postcranial dimensions are tabulated. Ferrets show a high degree of sexual dimorphism, with discriminant analysis correctly classifying 95% of all specimens to sex. Ferrets also exhibit north-south clinal variation in size, but they do not appear to exhibit variation based on species of *Cynomys* associate. The taxonomic relationship among ferrets and close relatives is described.

The black-footed ferret (*Mustela nigripes*) is a medium-sized musteline that is listed as endangered throughout its former range and currently receives full protection under the U.S. Endangered Species Act of 1973 (16 USC 1531 et. seq.). Endemic to North America, black-footed ferrets formerly occupied an extensive range from the Great Plains of Canada to intermontane regions of the interior Rocky Mountains and southwestern United States. The species is currently known from only one population restricted to an approximately 150 sq km area in northwestern Wyoming (Fig. 1). Decline of the black-footed ferret over the last 50 years is attributed to the often systematic eradication of its principal prey and associate, the prairie dog (*Cynomys spp.*), which is often viewed as an agricultural pest throughout the West. Prairie dogs are semifossorial colonial rodents (Sciuridae) that offer an abundant source of prey and burrows for ferret shelter.

Fig. 1. Historic range of the black-footed ferret (shaded area) compared with the current known range (dot).

Because black-footed ferrets are primarily nocturnal and spend much of their time underground, they seldom were observed in the wild by naturalists until recent technologies, specifically the high-intensity portable spotlight, made observation possible. Few details of the species biology were known until a small population in Mellette County, South Dakota, was studied from 1964 to 1974. Prior to that time information on distribution and

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specimens of ferrets were collected sporadically by commercial trappers, museum collectors, or federal and state rodent and predator control agents of the U.S. Fish and Wildlife Service (formerly the Biological Survey [BSC] and Bureau of Sport, Fisheries, and Wildlife [BSFW]). Specimens are therefore few and scattered among many collections.

Records of *M. nigripes* specimens and sight reports have been compiled for some states, but no comprehensive record of black-footed ferret distribution based on specimens exists other than Hall (1981). Some authors have included measurements from limited samples, but no systematic analysis based on a large sample has been made. The present study is based on a comprehensive examination and analysis of black-footed ferret remains and literature and describes the paleobiology, distribution, and skeletal morphometry of *M. nigripes*.

MATERIALS AND METHODS

Sixty-eight mammal collections were contacted and 48 of them reported having *M. nigripes* in their collections. Of these, eight collections were examined and measured. Collection data were supplemented by a thorough literature review. Evidence of ferrets was confirmed either by the presence in museums of specimens (skins, skeletal material) of *M. nigripes* or by observations of ferrets in hand reported in the literature by biologists familiar with the species. Some literature reports, therefore, include live-captured or killed animals that were not collected or preserved as museum specimens. Sight reports or secondary sources, however authentic, were not included.

Collections containing black-footed ferrets are listed below. Asterisks denote collections from which specimens were measured.

AMNH—American Museum of Natural History, New York*
ANSP—Academy of Natural Sciences, Philadelphia
AUG—Augustana College, Sioux Falls, South Dakota
BMS—Buffalo Museum of Science, Buffalo, New York
BNP—Badlands National Park, Interior, South Dakota
BSC—Biological Services Collection, Fort Collins, Colorado*
CDOW—Colorado Division of Wildlife, Denver
CMNH—Carnegie Museum of Natural History, Pittsburg
CSU—Colorado State University, Fort Collins
CU—Cornell University Division of Biological Sciences, Ithaca, New York
DMNH—Denver Museum of Natural History, Denver, Colorado*
FMNH—Field Museum of Natural History, Chicago
HM—Hastings Museum, Hastings, Nebraska
ISU—Iowa State University, Ames
KSU—Kansas State University, Manhattan
KUMNH—University of Kansas, Lawrence*
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts*
MDFWP—Montana Department of Fish, Wildlife and Parks, Bozeman*
MHM—Minnilusa Pioneer Historical Museum, Rapid City, South Dakota
MSU—Montana State University, Bozeman
NDSHS—North Dakota State Historical Society Museum, Bismarck
NGFP—Nebraska Game, Fish, and Parks, Lincoln
NMC—National Museum of Natural Sciences, Ottawa, Ontario
NSCM—Northwestern State College, Alva, Oklahoma
NYZ—New York Zoological Society, Bronx, New York
NZP—National Zoological Park, Washington, D.C.
OSU—Oklahoma State University, Stillwater
OU—University of Oklahoma, Norman
PAT—Patuxent Wildlife Research Center, Laurel, Maryland
ROM—Royal Ontario Museum, Toronto
SDNHM—San Diego Natural History Museum, San Diego, California
SNMH—Saskatchewan Museum of Natural History, Regina
SYR—State University of New York, Syracuse
SZCM—State Zoological Collection, Munich, German Federal Republic
UCB—University of California, Berkeley
UCM—University of Colorado Museum, Boulder*
UMMZ—University of Michigan Museum of Zoology, Ann Arbor
UMMNH—James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis
UND—University of North Dakota, Grand Forks
UNSM—University of Nebraska State Museum, Lincoln
USD—University of South Dakota, Department of Zoology, Vermillion
USNM—United States National Museum, Washington, D.C.*
UW—University of Wyoming, Laramie.
UWZM—University of Wisconsin Zoological Museum, Madison
WGF—Wyoming Game and Fish Department, Cheyenne
WHO—W. H. Over Museum, University of South Dakota, Vermillion
YPM—Peabody Museum, Yale University, New Haven, Connecticut
ZSP—Zoological Society of Philadelphia

Record localities are listed in Table 6 as they appeared on specimen labels or in the literature, with any comments or clarifying notes included in the text or remarks. Specimen label data were organized by collection date

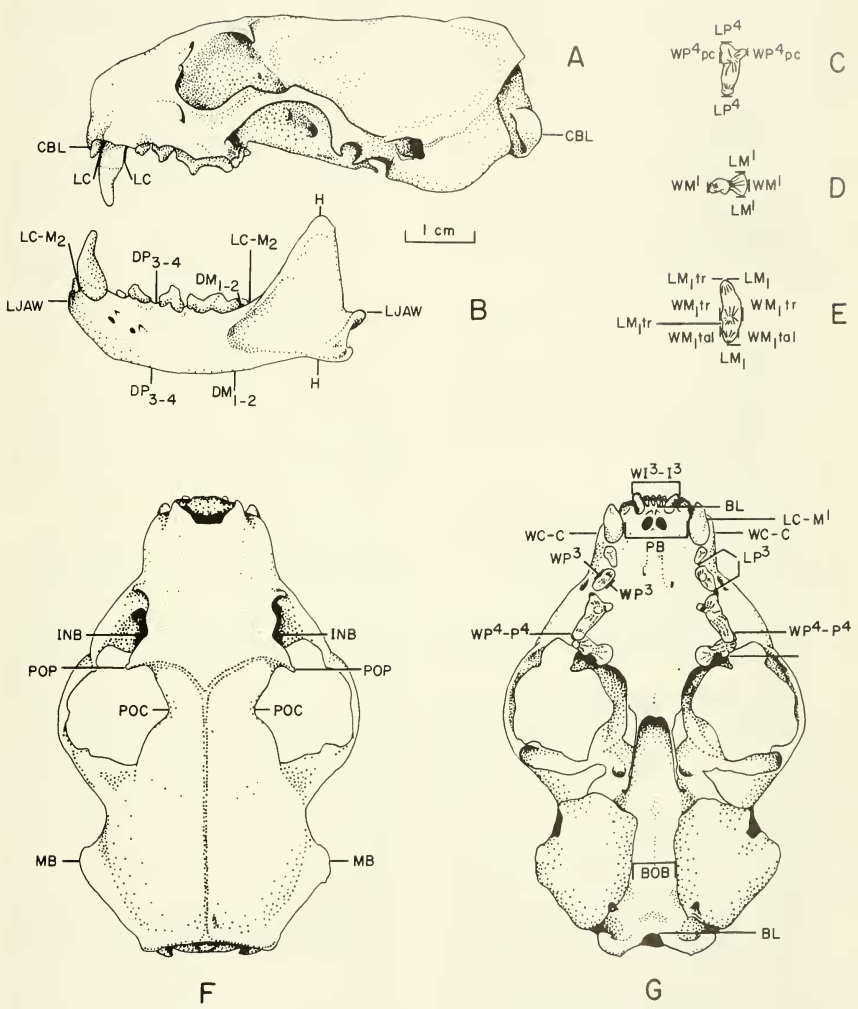

Fig. 2. Skull and mandible of black-footed ferret (Ad. ♂, Baca County, Colorado. DMNH 2248) showing measurements taken. A, Lateral view of skull. B, Lateral view of mandible. C, Occlusal view of P^4. D, Occlusal view of M^1. E, Occlusal view of M_1. F, Dorsal view of skull. G, Ventral view of skull. For symbols see Materials and Methods.

and state or province of collection. Localities (where known) were plotted on maps using dark circles for precise locations and open circles where location was known only to county.

Specimens with one exception were measured by E.A. These included 120 recent skulls, (72 of known sex), 17 skeletons, and 55 fossil (Pleistocene to Holocene) specimens. In addition, 19 skulls and one skeleton of the Siberian polecat (*M. eversmanni*), a possible Asiatic conspecific of the black-footed ferret, were also measured. Data on external measurements were taken directly from skin tags

and were supplemented by field measurements of live-caught known adult ferrets from the extant population at Meeteetse, Wyoming, from 1982 to 1984.

Measurements of skeletal material were made with vernier calipers to the nearest 1/10 mm. Material was separated by state, species of prairie dog in the locality collected (from the literature), and sex, if known. Figure 2 shows points between which cranial measurements were taken (after Anderson 1970). Cranial measurements taken included:

1. Condylobasal length (CBL). The least distance from a line connecting the posteriormost parts of the occipital condyles to the anteriormost parts of the premaxillae.
2. Basilar length of Hensel (BL). Least distance from a line connecting the anterior border of the foramen magnum to the posterior margin of the first upper incisors.
3. Rostral breadth (WC-C). Width across the rostrum above the canines.
4. Bimolar breadth (WP^4-P^4). Greatest width across the hind cheek teeth measured at the posterior margin of P^4 and the anterior margin of M^1.
5. Interorbital breadth (INB). Least distance across the frontal bones at the fronto-maxillary suture.
6. Postorbital breadth (POP). Greatest width across the postorbital processes.
7. Postorbital constriction breadth (POC). Least width across the frontal bones behind the postorbital processes.
8. Mastoid breadth (MW). Greatest width across the mastoid processes perpendicular to the long axis of the skull.
9. Mandible length (LJAW). Total length from the symphysis at the alveolus of I_1 to the most distant edge of the condyle.
10. Mandible height (H). From the lower border to the tip of the coronoid process.
11, 12. Ramus depth ($DP_{3\text{-}4}$, $DM_{1\text{-}2}$). Depth of the jaw between $P_{3\text{-}4}$ and $M_{1\text{-}2}$ measured from the level of the alveoli to the lower border.
13. Maxillary tooth row length ($LC\text{-}M^1$). Least distance from the anterior border of the canine at the alveolus to the posterior border of M^1 at the alveolus.
14. Mandibular tooth row length ($LC\text{-}M_2$). Least distance from the anterior border of the canine at the alveolus to the posterior border of M_2 at the alveolus.
15. Incisor breadth (WI^3-I^3). Least width from the buccal side of right I^3 to the buccal side of left I^3.
16. Canine length (LC). The least distance between the anterior and posterior edges of the canine at the level of the alveolus.
17. Canine breadth (WC). Transverse width of the canine at the level of the alveolus.
18, 19. Premolar length (LP^3, LP^4). Least distance from the anterior to the posterior edges of the premolars measured on the buccal side in the plane of the tooth row.
20. Premolar breadth (WP^3). Transverse width of P^3 measured at the center of the cusp.
21. Breadth of protocone of P^4 (WP^4pc). Greatest transverse width from the buccal border of the tooth to the edge of the protocone.
22. Upper molar breadth (WM^1).Greatest transverse width M^1.
23. Upper molar length (LM^1inner). Greatest anterior-posterior length of the inner lobe of M^1.
24. Length of M_1 (LM_1). Greatest anterior-posterior length of M_1 measured on the lingual side.
25. Trignoid length of M_1 (LM_1tr). From the posterior edge of the protoconid to the anterior edge of the tooth.
26, 27. Breadths of M_1 (WM_1 tr, WM_1 tal). Greatest width of the trigonid measured across the protoconid-metaconid; greatest width of the talonid measured across the hypoconid-entoconid.
28. Palatal breadth at canines (PB C-C). Width of palate between canines.
29. Basioccipital breadth (B OB). Breadth of basioccipital taken at midpoint between bullae.

Postcranial measurements taken included:

Humerus

Total length (TL). Greatest distance from the greater tuberosity to the medial epicondyle.

Proximal breadth (PB). Greatest width across the greater and lesser tuberosities.

Least shaft breadth (LSB). Least diameter of shaft.

Distal breadth (DB). Greatest width across the medial and lateral epicondyles.

Ulna

Total length (TL). Greatest distance from the top of the olecranon to the styloid process.

Breadth olecranon process (B 01 Pr). Maximum width of the olecranon.

Radius

Total length (TL). Greatest distance between the head and the styloid process.

Proximal breadth (PB). Maximum breadth across the head.

Distal breadth (DP). Maximum width of the distal end.

Femur

Total length (TL). Greatest distance from the head to the medial epicondyle.

Proximal breadth (PB). Maximum breadth between the greater trochanter and the head.

Least shaft breadth (LSB). Least diameter of the shaft.

Distal breadth (DB). Greatest distance across the condyles.

Tibia

Total length (TL). Greatest distance between the lateral condyle and the medial malleolus.

Proximal breadth (PB). Maximum breadth between the medial and lateral condyles.

Distal breadth (DB). Maximum width across the distal end.

Fibula

Length (L). Total length between the lateral condyle and the lateral malleolus.

Calcaneum

Length (L). Total length between the calcaneal atuberosity and the cuboid facet.

ASTRAGALUS
Length (L). Greatest perpendicular length of the bone.

BACULUM
Length (L). Greatest length of the bone from the proximal end to the base of the curve.

Specimens were placed in tentative age classes by the following criteria: (1) juvenile: cranial sutures open, deciduous dentition present, but permanent teeth beginning to erupt, epiphyses of long bones not fused; (2) young adult: internasal, nasomaxillary, basisphenoid, and basioccipital sutures fused but not obliterated, permanent dentition fully erupted except for upper canines, teeth unworn or only slightly worn, epiphyses of long bones fused, but sutures still visible; (3) adult: all cranial sutures obliterated, permanent dentition fully erupted, well-developed sagittal crest especially on males, epiphyseal sutures obliterated.

Statistical Methods

Analyses were performed on a Hewlett Packard 3000 computer using the Statistical Package for the Social Sciences (SPSS), including Discriminant Analysis and One-way Analysis of Variance (ANOVA). Linear discriminant analysis was performed between sexes using standardized measurements and confined to specimens of known sex. Juveniles were ommitted from the analysis to avoid allometric variation. Ranges, means, and standard deviations were calculated for both sexes of *M. nigripes*. Scattergrams and frequency diagrams were used to describe relationships between fossil and recent material and interspecies comparisons. A second linear discriminant analysis was performed on standardized cranial measurements of male and female ferrets to identify groups based on geographic variation and subgenera of prairie dog associate. One-way analysis of variance (ANOVA) was used to explore further variation of individual variables with regard to geographic clinal variation.

DESCRIPTION

Mustela nigripes (Audubon & Bachman)

Putorius nigripes Audubon & Bachman 1851: 297. Type locality Ft. Laramie, Goshen Co., Wyoming.
Mustela nigripes Miller 1912: 102. First use of binomial. No subspecies are recognized.

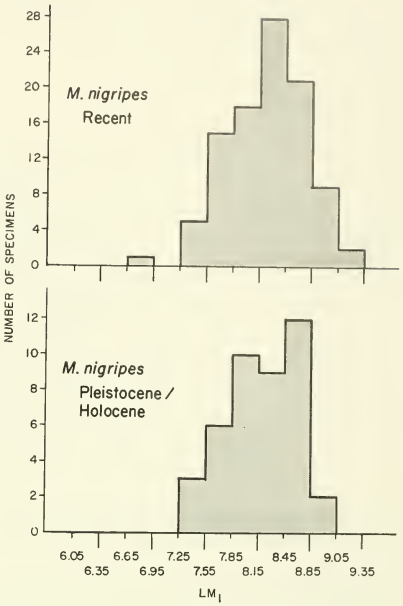

Fig. 3. Frequency histogram of length of M_1 for Recent, Pleistocene, and Holocene specimens.

DIAGNOSIS.—*Mustela nigripes* is a mink-sized mustelid weighing 645–1125 g. Upper parts yellowish buff, occasionally whitish, especially on the face and venter; feet black; black mask across the eyes, particularly well defined in young animals; tail black tipped. Skull is relatively short and broad; mastoid process is notably angular (Hillman and Clark 1980). Closely resembles *M. eversmanni*, the steppe ferret of Eurasia. Differs from *M. putorius*, the European ferret, and *M. vison*, the American mink, in being light colored with black markings; the latter two species are uniformly dark colored, and *M. p. furo*, the domestic ferret, is uniformly light colored, often albinistic.

Morphometry

Data on external measurements for Recent material were taken directly from skin tags and are supplemented with field measurements of live-caught juvenile and adult ferrets from Meeteetse from 1982 to 1984. Average (± S.D.) and extreme external measurements

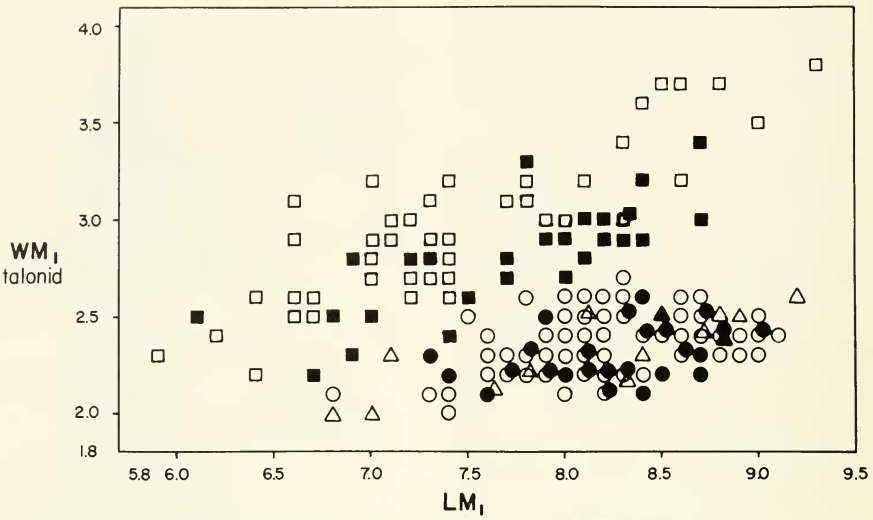

Fig. 4. Relationship between the width of M_1 talonid and the length of M_1 for *Mustela nigripes* (circles), *M. eversmanni* (triangles), and *M. vison* (squares) for Recent (open symbols) and Pleistocene (solid symbols) material.

in mm for adults are: Adult males (skin tags): total length (n=20) 533.8 ± 28.98, 490–600; tail (n=19) 123.0 ± 10.47, 107–140; hind foot (n=19) 61.4 ± 5.46, 51–70. Adult males (Meeteetse, field measured): total length (n=12) 566.8 ± 29.00, 517–615; tail (n=12) 137.0 ± 8.95, 119–148; hind foot (n=12) 64.1 ± 3.17, 59–65; ear (n=12) 28.2 ± 2.45, 25–34; weight (n=13) 1034.3 ± 60.18, 915–1125. Adult females (skin tags): total length (n=7) 501.1 ± 13.79, 479–518; tail (n=7) 119.0 ± 8.46, 109–132; hind foot (n=7) 59.8 ± 2.67, 56–63. Adult females (Meeteetse, field measured): total length (n=21) 532.0 ± 17.00, 496–565; tail (n=22) 132.2 ± 7.62, 120–141; hind foot (n=21) 57.2 ± 2.90, 51–62; ear (n=21) 25.6 ± 1.55, 23–28; weight (n=31) 703.5 ± 128.36, 645–850.

Young of the year measured in August and September are classified as juveniles and all others as adults. Juvenile males caught in October averaged total lengths of 578.0 ± 16.11 mm and weighed 943.5 ± 134.27 g. Juvenile females were 536.4 ± 22.20 mm in total length and weighed 700.6 ± 36.60 g. These measurements fall within adult ranges, indicating juveniles are externally as large as adults by about the time they reach independence in October. Differences between museum and field-measured groups are probably related to measuring errors under field conditions with live animals and do not represent real size differences between specimens. Since field measurements were taken consistently, their relative values are similar.

Comparisons of the Pleistocene material with Recent specimens showed no differences in size or morphology. Of the nine mandibular characters for which data were available, none significantly differed from recent material in frequency plots (Fig. 3) or in scattergrams (Figs. 4, 5, 6). Data on fossil remains was most consistently available for mandibular and dental characters. Only 29 values for 16 cranial characters from 11 specimens were available. Table 1 shows cranial measurements for Pleistocene material assigned to sex based on the discriminant analysis for Recent material.

The skull of *M. nigripes* is relatively short and broad with large postorbital processes and widely spreading zygomatic arches. It has a short convex rostrum, a slight facial angle, obliquely flattened auditory bullae, and a narrow basioccipital region. In adult males the sagittal and lambdoidal crests are well developed and the mastoid processes are angular and projecting. The postorbital constriction is pronounced, unlike the condition in *M. puto-*

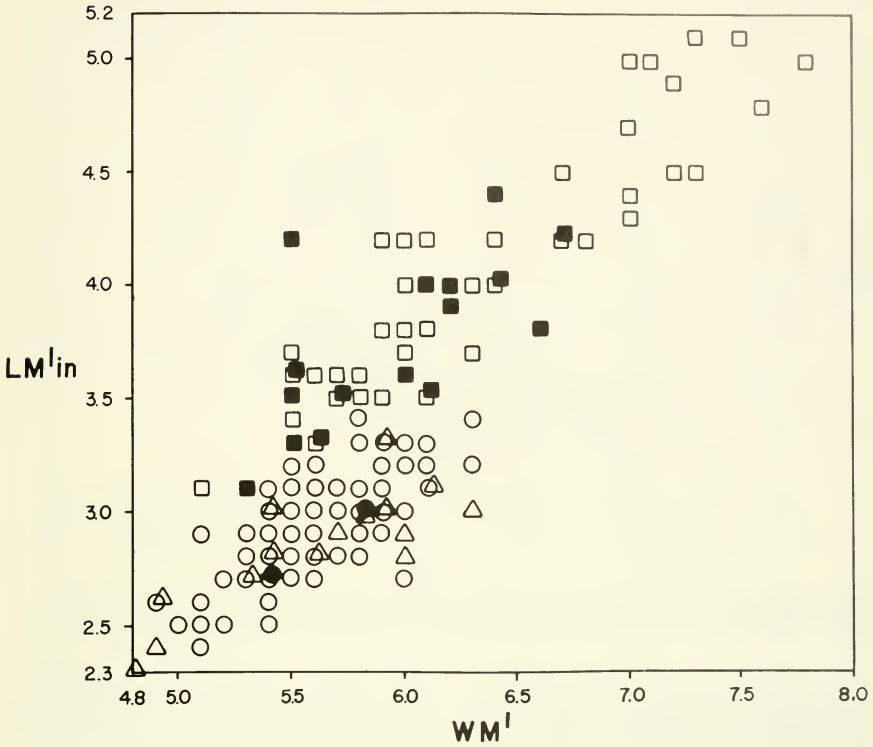

Fig. 5. Relationship between the length of M^1inner lobe and the width of M^1 for *Mustela nigripes* (circles), *M. eversmanni* (triangles), and *M. vison* (squares) for Recent (open symbols) and Pleistocene (solid symbols) material.

TABLE 1. Mandibular and dental dimensions for Pleistocene specimens of *M. nigripes*. For symbols used in Column 1 see Cranial Measurements under Materials and Methods.

	Sex	Number	Minimum	Mean	Maximum	S. D.
LJAW	M	4	41.9	42.2	42.6	0.29
	F	9	34.7	38.0	40.3	1.96
H	M	6	19.5	20.5	21.8	0.86
	F	7	16.1	18.5	19.7	1.25
DP_{3-4}	M	18	8.4	9.0	10.0	0.43
	F	14	6.5	7.5	8.4	0.54
DM_{1-2}	M	18	7.8	8.7	9.9	0.51
	F	15	6.8	7.7	9.1	0.54
LC-M_2	M	8	23.9	24.9	25.3	0.47
	F	9	20.4	22.1	23.5	0.96
LM_1	M	19	7.8	8.5	9.0	0.29
	F	18	7.3	7.9	8.4	0.34
LM_1tr	M	19	5.6	6.1	6.3	0.21
	F	17	5.2	5.6	6.2	0.25
WM_1tr	M	16	2.8	3.2	3.6	0.22
	F	15	2.5	2.8	3.1	0.23
WM_1tal	M	19	2.2	2.3	2.6	0.17
	F	18	2.0	2.2	2.3	0.09

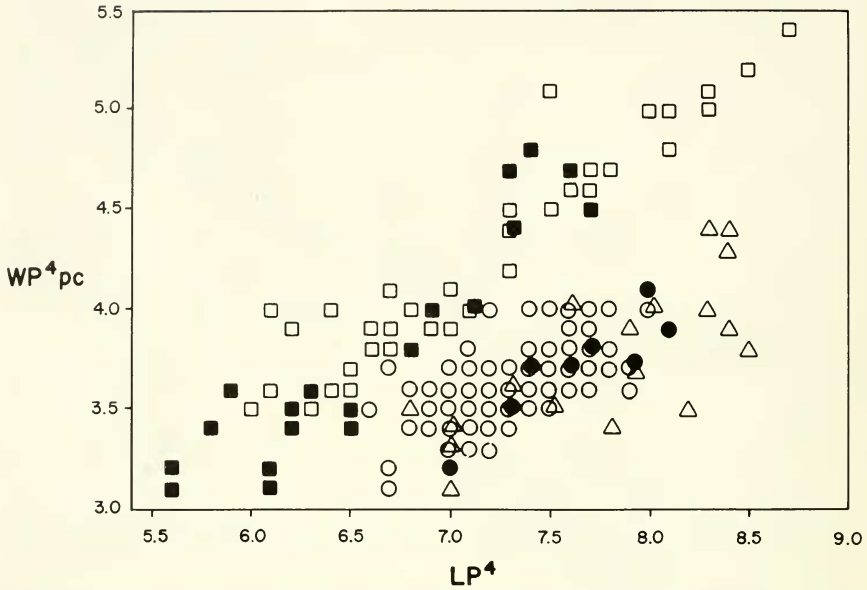

Fig. 6. Relationship between the width of P^4 protocone and the length of P^4 for *Mustela nigripes* (circles), *M. eversmanni* (triangles), and *M. vison* (squares) for Recent (open symbols) and Pleistocene (solid symbols) material.

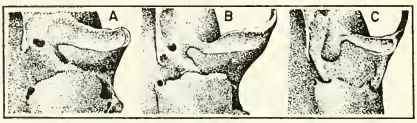

Fig. 7. Portion of basicranium of *Mustela nigripes* showing the well-defined tube enclosing the foramen ovale and extending posterolaterally to the anterior margin of the auditory bulla. Compared with *M. vison*. A, *M. nigripes* from Little Box Elder Cave (UCM 21952). B, *M. nigripes* Recent (UCM-S 263). C, *M. vison* Recent (UCM 7449) (from Anderson 1968).

rius. The broad palate extends beyond the last molar. Anderson (1968:32) described the characteristic basicranium as follows:

> Black-footed ferret skulls have a well-defined tube enclosing the foramen ovale and extending postero-laterally to the anterior margin of the auditory bulla. Anteriorly the tube is emarginate with the post-glenoid process and opens just anterior to the pterygoid process. The foramen ovale pierces the alisphenoid; immediately anterior to it is the foramen rotundum.

The tube is absent in mink (Fig. 7) and is useful in distinguishing the two species.

Sagittal crest formation has been used to age ferrets in the field with some success (Thorne et al. 1985). Animals of both sexes may be classed as either juveniles or adults on the basis of the definition and sharpness of the crest, which is generally not prominent in animals less than 6 months in age but fairly defined in one-year-old animals. It initially increases in prominence with age and then flattens out.

The mandible is relatively short and thick, and the inferior margin at the angle is broad and flattened. The masseteric fossa extends anteriorly to the middle of the talonid of M_1. The mental foramina, usually four in number, are located below P_{2-3} and P_{3-4}. Average and extreme cranial measurements are shown in Table 2.

The dental formula of *M. nigripes* and the other ferrets and mink is i 3/3, c 1/1, p 3/3, m 1/2, for a total of 34 teeth that are set close together but do not overlap. The incisors are small and the upper ones are set in a straight row separated from the canines by a short diastema; the lower incisors are crowded with

TABLE 2. Cranial and dental dimensions for *M. nigripes* (Recent).

	Sex	N	Minimum	Mean	Maximum	S.D.
CBL	M	45	64.1	68.0	70.8	1.62
	F	23	58.1	63.3	67.5	2.47
BL	M	44	58.6	62.4	65.5	1.56
	F	24	53.0	58.0	61.7	2.25
WC-C	M	47	16.0	17.7	19.0	0.65
	F	24	14.2	16.0	17.2	0.77
WP^4-P^4	M	48	22.3	24.3	25.9	0.77
	F	24	20.4	22.6	23.6	0.98
INB	M	49	16.2	17.6	19.5	0.76
	F	24	14.8	15.9	17.4	0.65
POP	M	48	19.8	21.7	23.8	1.24
	F	24	18.4	19.6	22.5	1.04
POC	M	46	9.8	12.7	15.3	1.01
	F	24	10.0	12.1	14.5	1.18
MW	M	46	30.4	36.5	40.1	1.58
	F	23	28.8	33.7	36.3	1.65
LC-M^1	M	46	19.1	20.3	21.9	0.62
	F	24	17.5	19.0	20.8	0.79
LC	M	47	3.7	4.3	4.8	0.20
	F	24	3.2	3.8	4.2	0.24
WC	M	47	3.0	3.3	3.6	0.17
	F	24	2.7	2.9	3.2	0.14
LP^4	M	49	7.0	7.5	8.0	0.24
	F	24	6.7	7.1	7.5	0.23
WP^4_{pc}	M	49	3.3	3.7	4.0	0.18
	F	24	3.1	3.5	3.8	0.17
WM^1	M	49	5.2	5.7	6.3	0.26
	F	24	4.9	5.4	5.8	0.25
LM^1	M	49	2.7	3.0	3.4	0.18
	F	23	2.4	2.8	3.1	0.21
LJAW	M	47	40.4	43.1	45.6	1.34
	F	24	35.2	39.5	43.1	1.90
H	M	45	18.7	21.0	22.2	0.75
	F	24	17.0	19.2	21.4	1.12
$DP_{3\text{-}4}$	M	46	7.8	8.7	9.5	0.39
	F	24	7.1	7.9	8.8	0.44
$DM_{1\text{-}2}$	M	47	7.7	9.0	10.0	0.48
	F	24	7.1	8.1	9.1	0.52
LC-M_2	M	46	23.2	24.6	26.1	0.66
	F	23	20.5	22.7	24.4	0.93
LM_1	M	48	7.7	8.4	9.1	0.37
	F	24	6.8	7.9	8.4	0.40
LM_1tr	M	47	5.6	5.9	6.4	0.20
	F	23	5.1	5.5	6.0	0.22
WM_1tr	M	48	2.7	3.1	3.5	0.16
	F	24	2.6	2.9	3.2	0.17
WM_1tal	M	47	2.2	2.4	2.6	0.11
	F	24	2.0	2.2	2.8	0.17
WI^3-I^3	M	38	6.0	6.5	7.2	0.29
	F	23	5.1	6.0	6.6	0.39
WBC	M	35	8.3	9.4	10.3	0.46
	F	30	7.7	8.6	9.4	0.45
BOB	M	37	6.1	7.2	9.1	0.67
	F	32	5.9	6.7	7.7	0.48
LP^3	M	40	3.6	3.9	4.2	0.16
	F	35	3.2	3.7	4.0	0.20
WP^3	M	40	2.0	2.2	2.5	0.13
	F	35	1.7	2.1	2.3	0.14

I_2 set back of I_1 and I_3. The canines are relatively large and slightly curved. The anterior premolars (P^{2-3}, P_{2-4}) are double-rooted, relatively short and broad, and single-cusped. The upper carnassial (P^4) is trenchant with a relatively small protocone; the width of the tooth across the protocone is less than that of mink (Fig. 22). P^4 is longer than the width of M^1. The upper molar (M^1) has the characteristic hourglass shape of the Mustelinae, but the inner lobe is not as expanded as that of mink (Fig. 5). There is no trace of a metaconid on the lower carnassial (M_1) and the trigonid is longer than the talonid; ferrets have a narrower talonid than do mink (Fig. 4). M_2 is relatively small, and circular in shape. Figures 4, 5, and 6 show that measurements of *M. nigripes* fall within the range of *M. eversmanni*.

No supernumerary teeth were observed. In a few mandibles P_2 (2 specimens) or M_2 (4 specimens) was absent and the alveolus closed; whether the tooth had been lost and the alveolus closed during the life of the animal or whether the tooth had never erupted could not be determined. Only one specimen (USNM 21976) had an abcessed tooth (P^4). Ruprecht (1978) noted deviations in the number of teeth in *M. putorius* in Poland and Holland. With advanced age the tooth cusps become worn smooth and the canines, perhaps broken earlier in life, are stubby and rounded. No studies are available on the sequence of eruption of the teeth of *M. nigripes*, nor have there been any studies on age determination by counting the annuli in tooth cementum or using radiographs to determine the size of the pulp cavity of the canine. Average and extreme dental measurements are shown in Table 2.

The appendicular skeleton of the black-footed ferret is unspecialized and shows no extreme modifications as are seen in badgers and otters. The shafts of the limb bones are relatively straight, the proximal and distal ends are not greatly expanded, and processes are not overly developed. The calcaneum has a well-developed trochlear process, and the posterior articular surface is rounded and smooth (Stains 1966). Only a few limb bones of *M. nigripes* have been recognized in Pleistocene faunas (Little Box Elder, Jaguar, and Isleta caves); their measurements fall within those of Recent specimens. Table 3 gives postcranial dimensions of Recent *M. nigripes*. Compared with mink, the limb bones of ferrets tend to be more rugose and show less curvature, but it is difficult to separate the two species when only limb bones are available.

The baculum of *M. nigripes* is similar to that of mink in having the distal end hooked sharply backward. In young animals the proximal end is a simple, laterally flattened base that with age develops a collar and becomes quite rugose. The ventral groove extends more than half the length of the shaft (Burt 1960). Eight bacula were examined and measured; the Pleistocene specimen from Isleta Cave (Fig. 8) was identical in size and morphology to the Recent material.

Life history

The black-footed ferret is a mostly nocturnal, solitary carnivore. The range of the black-footed ferret is sympatric with that of the prairie dog (*Cynomys*) throughout North America, and breeding populations of ferrets have only been found in association with prairie dog colonies (Linder et al. 1972, Forrest et al., *Black-footed ferret habitat*, 1985). Ferrets live in the burrows made by prairie dogs and exploit prairie dogs as their major food source (Sheets et al. 1972). Ferrets also eat lagomorphs, mice (cricetids), voles (microtines), ground squirrels and pocket gophers (geomyids), birds, and insects (Henderson et al. 1969; Clark et al. 1985).

Breeding occurs in March-April. Coitus lasts from 1.5 to 3 hours, and gestation is approximately 42–45 days (Carpenter and Hillman 1978). Litter sizes range 1–5 young and average 3.3–3.4/litter (Linder et al. 1972, Forrest et al., *Life history characteristics*, 1985). Juveniles first appear aboveground in late June. The sex ratio at this time is equal (Forrest et al., *Life history characteristics*, 1985).

Primary mortality sources for black-footed ferrets are unknown. Potential predators of ferrets include: badgers (*Taxidea taxus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), golden eagles (*Aquila chrysaetos*), great-horned owls (*Bubo virginianus*), and hawks (Henderson et al. 1969; Forrest et al. *Litter survey*, 1985). Forrest et al. (*Life history characteristics*, 1985) identified four major

TABLE 3. Postcranial dimensions, Recent *M. nigripes*. For symbols used in column 1 see Materials and Methods.

Bone	Sex	N	Minimum	Mean	Maximum	S.D.
HUMERUS						
TL	M	11	46.0	49.5	52.0	1.79
	F	2	45.5	46.2	47.0	—
PB	M	11	9.9	10.7	11.7	0.59
	F	2	10.0	10.2	10.4	—
LSB	M	10	3.5	3.8	4.1	0.20
	F	1	—	3.3	—	—
DB	M	11	12.3	13.0	13.8	0.57
	F	2	11.4	11.8	12.2	—
ULNA						
TL	M	10	44.4	46.6	48.6	1.36
	F	2	42.9	43.8	44.7	—
B 01 Pr.	M	11	5.5	5.7	6.2	0.30
	F	2	5.3	5.6	5.8	—
RADIUS						
TL	M	10	33.5	36.0	37.2	1.16
	F	2	32.9	33.9	34.9	—
PB	M	11	4.8	5.6	6.0	0.33
	F	2	5.1	5.4	5.6	—
DB	M	10	6.2	6.9	7.4	0.39
	F	2	6.2	6.4	6.6	—
FEMUR						
TL	M	11	47.1	51.3	53.7	2.05
	F	2	46.7	47.9	49.1	—
PB	M	11	11.7	12.7	13.5	0.59
	F	2	11.0	11.4	11.7	—
LSB	M	10	4.1	4.4	4.8	0.28
	F	2	3.9	4.2	4.4	—
DB	M	11	9.5	10.8	11.6	0.55
	F	2	9.4	9.9	10.4	—
TIBIA						
TL	M	11	48.3	51.5	54.4	1.75
	F	3	47.1	48.4	49.8	1.36
PB	M	11	9.8	10.7	11.4	0.51
	F	3	9.2	10.1	10.6	0.75
DB	M	11	7.1	7.8	8.1	0.32
	F	3	7.1	7.3	7.5	0.21
T. L. FIBULA	M	10	44.9	47.2	48.7	1.11
	F	1	—	43.1	—	—
T. L. CALCANEUM	M	10	13.0	13.6	14.8	0.49
	F	1	—	12.3	—	—
T. L. ASTRAGALUS	M	8	8.5	8.9	9.3	0.32
	F	1	—	7.6	—	—
T. L. BACULUM	M	8	31.2	36.9	40.0	2.64

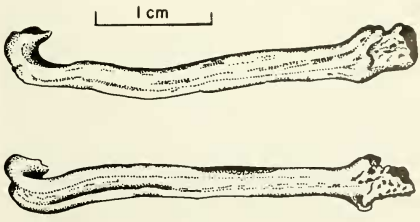

Fig. 8. Baculum of *M. nigripes* (Isleta Cave A 2967; total length 35.5 mm).

sources of mortality (predation, disease, man-caused, and resource related) and suggested from comparative studies of other *Mustela* species that average life span of ferrets in the wild is probably less than one year; there is preliminary evidence of high juvenile mortality at Meeteetse.

Forrest et al. (*Black-footed ferret habitat*, 1985) estimate ferret distribution at Meeteetse at about 40–60 ha/ferret and noted that large prairie dog colonies (greater than 40 ha) support most female ferrets with litters. Large

TABLE 4. Black-footed ferret remains from Pleistocene, Early Holocene, and archeological faunas and steppe ferret remains from the Pleistocene of Alaska.

Fauna	Location	Age	Ferrets	
			Minimum number	Number of specimens
Cudahy	Kansas, Meade Co.	Late Irvingtonian	1	1
Adams Co.	Nebraska, Adams & Clay Cos.	? Late Illinoian	1	1
Medicine Hat	Alberta, Canada	Sangamonian	1	1
Moore Pit	Texas, Dallas & Denton Cos.	> 30,000 yrs. B.P.	1	1
"Citellus" beds	Nebraska, Lincoln Co.	28,000–30,000 yrs. B.P.	1	3
Cottonwood Canyon	Nebraska, Lincoln Co.	28,000–30,000 yrs. B.P.	1	1
Smith Falls	Nebraska, Cherry Co.	Wisconsin	1	1
Harlan Co. Dam Site	Nebraska, Harlan Co.	Wisconsin	1	2
January Cave	Alberta, Canada	23,100–33,500 yrs. B.P.	2	7
Little Box Elder Cave	Wyoming, Converse Co.	9,000- > 30,000 yrs. B.P.	15	40
Chimney Rock Animal Trap	Colorado, Larimer Co.	11,980 ± 180	1	1
Burnet Cave	New Mexico, Eddy Co.	11,170 ± 360	1	1
Jaguar Cave	Idaho, Lemhi Co.	10,370 ± 350	2	12
Little Canyon Creek Cave	Wyoming, Washakie Co.	10,170 ± 250	1	1
Orr Cave	Montana, Beaverhead Co.	Late Pleistocene	1	1
Old Crow River, Location 65	Yukon Territory, Canada	Late Pleistocene	1	1
Isleta Cave	New Mexico, Bernalillo Co.	Late Pleistocene/ early Holocene	2	6
Red Willow	Nebraska, Red Willow Co.	Late Pleistocene/ early Holocene	1	1
Moonshiner Cave	Idaho, Bingham Co.	Early Holocene	1	2
Atlatl Cave	New Mexico, San Juan Co.	2,000–3,000 yrs. B. P.	1	1
Ashislepha Shelter	New Mexico, San Juan Co.	Archaic	1	1
Upper Plum Creek	Colorado, Las Animas Co.	570 ± 50–1,050 ± 80 AD	2	4
Mustela eversmanni beringiae				
Fairbanks	Alaska, near Fairbanks	Late Pleistocene	2	3

clusters of prairie dog colonies appear necessary to support populations. The lack of such colonies in highly developed prairie lands is suspected as the principle cause of ferret endangerment, although possible catastrophic losses of prey base due to sylvatic plague in prairie dogs has also been discussed (Hubbard and Schmitt 1984).

DISTRIBUTION

Pleistocene and Paleo-Indian Distribution

Ferrets have been identified from 21 Pleistocene and Holocene faunas in North America (Table 4). Two ferret species, *Mustela eversmanni* from Fairbanks, Alaska (Anderson 1977) and *M. nigripes* are recognized. Six occurrences of *M. nigripes* are outside the historic range (Fig. 9) of this species.

The earliest occurrence of *M. nigripes* is uncertain, but the species has probably been present in North America since the Sangamonian about 100,000 years ago. The specimen from the Cudahy fauna, an isolated left M^1 (University of Michigan Museum of Vertebrate Paleontology #38341) was originally identified as *Mustela* cf *vison* by Getz (1960), who noted slight differences between it and the comparative material. Later Hibbard (1970) referred the specimen without comment to *M. nigripes* and Corner (1977) followed this designation. Examination of the tooth showed the presence of an incipient metaconid, a characteristic of mink but not ferret. Measurements of the tooth of the two species are not diagnostic. The age of the Cudahy fauna is Irvingtonian (Type 0, Pearlette Ash, 600,000 yrs B.P.), and the habitat was marshy with permanent, slow-moving streams; numerous species of aquatic and semiaquatic animals have been identified. Mink have been identified from other Irvingtonian faunas, ferrets have not. Thus, the identity of this tooth remains questionable. We follow Getz's (1960)

Prey species	Remarks	References
No *Cynomys*, many spp. rodents	? Id. Originally identified as *M. vison*; see text	Getz 1960, Hibbard 1970
		L. Martin, pers. comm.
Cynomys leucurus	Grassland, warmer than today	Stalker et al. 1982
No *Cynomys*, many spp. rodents	Originally identified as *M. vison*	Slaughter 1966
No *Cynomys*, many spp. rodents	Age originally thought to be Sangamonian	Dreeszen 1970 Corner, pers. comm.
No *Cynomys*, rodents abundant	May be "Citellus" zone in part; open prairie	R. G. Corner, pers. comm.
Cynomys sp.	Steppe	Voorhies and Corner, in press
No *Cynomys*, many spp. rodents	Articulated skull and mandible; open prairie	R. G. Corner, pers. comm.
Cynomys leucurus		J. Burns, pers. comm.
Cynomys leucurus		Anderson 1968, 1974
Cynomys sp.		Hager 1972
Cynomys ludovicianus	? Id. Juvenile; deciduous dentition	Schultz and Howard 1935
No *Cynomys*, many spp. rodents	Outside historic range	Kurtén and Anderson 1972
No *Cynomys*, many spp. rodents		D. Walker, pers. comm.
No *Cynomys*	Outside historic range	Guilday and Adam 1967
No *Cynomys*	Outside historic range, cool grassland	C. R. Harington, pers. comm.
Cynomys gunnisoni		Harris and Findley 1964
Cynomys ludovicianus		Corner 1977, pers. comm.
No *Cynomys*, many spp. rodents	Carnivore trap; outside historic range	White et al. 1984
	Specimen burned	J. Hubbard, pers. comm.
Cynomys gunnisoni		W. Gillespie, ms. and pers. comm.
104 *Cynomys ludovicianus*	1 specimen burned, 2 found in bone cache	Anderson, ms.
No *Cynomys*, many spp. rodents, lagomorphs	Cool grassland. Only record of *M. e.* in North America	Anderson 1977

designation of *M.* cf *vison*. The next earliest record of ferret may be late Illinoian/early Sangamonian (Adams/Clay counties, Nebraska, exact age uncertain; the specimens from the "Citellus" beds were originally thought to be the same age but are now regarded as late Wisconsinan in age) or Sangamonian (Medicine Hat), about 100,000 yrs B.P. By the late Wisconsin/early Holocene (15,000–8,000 B.P.), ferrets ranged across the Great Plains west to Montana (Orr Cave) and Idaho (Jaguar, Moonshiner caves) and even as far north as Yukon Territory (Old Crow). At most sites only a few bones representing one individual have been found, but at Little Box-Elder Cave at least 40 specimens and 15 individuals (based on left mandibles) have been identified. The site, in the foothills of the Laramie Mountains, contains a large number of prey animals including *Cynomys* cf *leucurus* (n=77+). Prairie dogs have been found in 10 of the faunas containing ferrets. The other sites did not contain prairie dogs, but various rodent and lagomorph species were abundant. At two archeological sites, Atlatl Cave and Upper Plum Creek Rockshelter, burned ferret bones were found, indicating their possible use by Paleoindians.

During the late Pleistocene the steppe ferret, *M. eversmanni*, ranged east to Beringia, the vast unglaciated land mass that extended from northeastern Siberia to western Alaska. Its remains have been found in deposits near Fairbanks, Alaska (Anderson 1973, 1977). The specimens, a partial skull and two mandibles, are characterized by large size, broad facial region, massive postorbital processes, pronounced postorbital constriction, crowded tooth row, and enlarged canines. Measurements exceeded those of *M. eversmanni michnoi*, the largest extant subspecies. Anderson (1977) described the material as a new subspe-

Fig. 9. Distribution of black-footed ferrets in Pleistocene, early Holocene, and archeological faunas compared with its historic range (1851–1920).

cies, *M. e. beringiae*, and noted that it is the first and only record of the steppe ferret in North America.

In the Old World ferrets are recognized in middle Pleistocene faunas in central Europe, but whether the fragmentary remains are of *M. putorius* or *M. eversmanni* is unknown. By the late Pleistocene remains of *M. putorius* are common in Eurasian cave faunas. *Mustela eversmanni* has been reported from late Pleistocene/Holocene faunas in Siberia, Crimea, and the Russian plains and from Holocene faunas in the Caucausus and central Asia (Vereshchagin and Baryshnikov 1984).

Early Historic Record

The first possible report of *M. nigripes* by a European may be attributed to Don Juan de Oñate, a Spanish explorer of what is now the southwestern U.S. in 1599.

> It is a land (New Mexico Territory) abounding in flesh of buffalo, goats with hideous horns, and turkeys; and in Mohoce there is game of all kinds. There are many wild and ferocious beasts, lions, bears, wolves, tigers, penicas, *ferrets*, porcupines, and other animals, whose hides they tan and use. (Bolton 1916: 217; italics ours).

Both domestic (*M. putorius furo*) and wild European polecats (*M. p. putorius*) were common in Europe at that time, so Oñate could have correctly identified the North American counterpart. It is possible he could have confused ferrets with other *Mustela* that have no comparable Old World counterparts, particularly the "bridled" weasels (color morphs of *M. frenata*: *M. f. arizonensis* and *M. f. neomexicana*) of the southwest. Since Mohoce (also "Moqui," the center of the Hopi nation, in the vicinity of present-day Walupi, Arizona) is within known black-footed ferret range, it appears equally likely that what Oñate described was in fact a black-footed ferret.

Several ethnographically known tribes were familiar with and used black-footed ferret skins in ceremonial dressings (Henderson et al. 1969, Clark 1975). Tribes with knowledge of black-footed ferrets ranged from the Navaho of northern Arizona and New Mexico to the Hidatsas of the upper Missouri River Basin (Table 5).

Ferrets were also reported in the records of the American Fur Company from 1835 to 1839 (Johnson 1969). Pratte, Chouteau, and Company of St. Louis listed pelts of 86 black-footed ferrets taken during this period. Trappers were familiar with mustelids ("weasels" are listed separately from ferrets in this tally) and probably accurately identified the species long before it was scientifically named and described by Audubon and Bachman (1851). It was Alexander Culbertson, a trapper, who first brought the species to the attention of Audubon. Known as the "French Fur Company," Pratte, Chouteau, and Company became the Western Department of the American Fur Company, concentrating most of their effort in the upper Missouri River basin. They operated for some time out of Ft. Kiowa near the junction of the White and Missouri rivers in present-day South Dakota (Morgan 1953). Their license was for "Sioux Country," which encompassed parts of present-day South Dakota, Montana, and Wyoming.

TABLE 5. Black-footed ferret specimens associated with ethnographically known Indian tribes.

Ethnographic tribe	Tribal name for BFFs	Specimen type	No. of specimens	Disposition	Citations
Blackfoot	?	chief's headdress	1	?	Homolka 1964
Cheyenne	?	chief's headdress	?	?	Henderson et al. 1969
Crow	?	medicine pouch	4	Chief Plenty Coups Museum, Pryor, Montana	
		medicine pouch	2	Plains Indian Museum, Cody, Wyoming	
		skin	2	Plains Indian Museum, Cody, Wyoming	
		skin	1	Colter Bay Indian Museum, Grand Teton National Park, Wyoming	
Hidatsas	"Tahu akukahak napish"				Bailey 1926
Mandan	"Nazi"				Bailey 1926
Navajo	"dlo'ii liz-hinii"	"pelts"	"several"		Fortenbery 1971, Halloran 1964
Pawnee	"ground dogs" in a mythical story; speaks of itself as "staying hid all the time"				Grinnell 1895, 1896
Sioux	"pispiza etopta sapa," "black-faced prairie dog"	skins, sacred tribal objects	2	St. Francis, South Dakota	Henderson et al. 1969

Recent Distribution

John James Audubon and John Bachman (1851) named and described *Mustela nigripes* from a specimen collected near Fort Laramie, in what is now Goshen County, Wyoming. This specimen was either lost or destroyed, and subsequently naturalists questioned whether the species actually existed (Gray 1865). Elliot Coues (1874:1), curator of the Smithsonian mammal collection, published a plea in the *American Sportsman* for additional specimens likely to be found "out on the plains in the prairie dog towns." Coues was rewarded with several specimens and accounts of black-footed ferrets, which he subsequently described (Coues 1877).

Table 6 gives a comprehensive listing of each known ferret specimen by state. Black-footed ferrets have been found with three species of *Cynomys*: *C. ludovicianus* (black-tailed prairie dog), *C. leucurus* (white-tailed prairie dog), and *C. gunnisoni* (Gunnison's prairie dog). Since *M. nigripes* distribution and abundance is highly dependent on prairie dog distribution and abundance, we include discussion of the past and present range of *Cynomys*. Because genetic "bottlenecks" occur when species numbers are low and may be critical for species survival (Soule 1980), an estimate of habitat available to ferrets based on prairie dog distribution at their lowest point is also given where known.

ARIZONA

Four specimens of *M. nigripes* are known for Arizona (Table 6, Fig. 10). The last specimen was collected in Coconino County in 1931. Two of these specimens from the U.S. National Museum were described by Young and Halloran (1952).

Historically two species of prairie dogs, *C. ludovicianus* and *C. gunnisoni*, inhabited Arizona. The ferrets were all collected within the range of *C. gunnisoni*. *Cynomys ludovicianus* was probably extirpated in Arizona as early as 1932 (Alexander 1932) and no longer exists in the state (Cockrum 1960). Current distribution of *C. gunnisoni* is also greatly reduced, although relict populations of sufficient size to support black-footed ferrets may persist in the northeastern corner of the state. The historic, as well as present area occupied by prairie dogs is unknown.

TABLE 6. Recent black-footed ferret specimen accounts by state, 1851–1984.

Year	Date	Disposition	County	Site	Sex	Skeleton	Crania	Skin
ARIZONA								
1917	Jan 19	USNM 228233	Apache	Springerville, 27 km NE	M		X	X
1929	Jan	USNM 248973	Coconino	Williams, N Red Lake	M		X	X
1931	Oct	UCB 55213	Coconino	Winona, 19 km W	F			
1931	Nov	UCB 55212	Coconino	Gov't. prairie near parks	—			
COLORADO								
ca 1876	—	Unknown (n = 3)	—	"Vicinity of Denver"	—			
ca 1877	—	Unknown	Larimer	Valley of the Cache La Poudre	—			X
1878	Apr	AMNH 24412	El Paso	—	—			
1887	Feb	MCZ B4184	Larimer	—	M		X	X
1887	Jan 6	ANSP 8640	Larimer	—	F		X	X
1887	—	ANSP 8641	Larimer	—	—			
1888	Apr	DMNH 653	Grand	Middle Park	M			X
1900	Apr 1	UWZ 11776	El Paso	Colorado Springs	M		X	X
1904	—	Unknown	El Paso	Clyde Station	—			
1905	Jan 16	UCM 10658	Teller	Divide Station	M		X	X
1905	Apr 14	UCM 10659	Baca	N of Springfield	F		X	X
1905	Sep 23	UCM 10660	El Paso	Lake Moraine	F		X	X
1909	Jan 2	UCM-W59	Larimer	Laramie R., 19 km S of Wyoming border	M		X	
ca 1910	—	Private Collection	Rio Blanco	Meeker, 2 km	—			
ca 1910	—	Private Collection	Rio Blanco	Meeker, 2 km	—			
1910	Mar	UCM-W232	Weld	Cornish, 13 km E	—			X
1912	May 5	DMNH 257	Denver	Denver, Park Hill	(F)		X	
1913		CSU	Larimer	—	—			X
1914	Mar 15	DMNH 1208	Adams	Barr	F		X	X
1914	Dec 16	DMNH 1558	Adams	Simpson	M		X	X
1914	Dec 16	DMNH 1559	Adams	Simpson	F		X	
1915	Mar 30	AMNH 41994	Adams	Simpson	F		X	
1915	Oct 31	DMNH 5792	Jefferson	Semper	M		X	X
1916	Feb 21	DMNH 1684	Adams	Simpson	M		X	X
1916	Feb 21	DMNH 1883	Adams	Simpson	F		X	X
1919	Nov	USNM 234118	Saguache	Del Norte, 24 km NW	M		X	X
1922	—	USNM 265540	Weld	E of Greeley	—			X
1923	May 13	DMNH 1987	Weld	Grover, 8 km S	M		X	X
1923	May 13	DMNH 6726	Weld	Grover, 8 km S	F			X
1924	Feb	DMNH 2024	Baca	Furnace Canyon	M		X	X
1924	Feb	DMNH 2247	Baca	Furnace Canyon	(M)		X	X
1924	Feb	DMNH 2248	Baca	Furnace Canyon	(M)		X	
1926	Nov	USNM 247073	Park	Hartsel, 11 km S	F		X	X
1928	Feb 9	DMNH 2371	Baca	Furnace Canyon	(M)		X	
1930	Feb 11	DMNH 4322	Adams	Denver, 16 km E	F			X
1934	Aug	UCM-W493	Montezuma	Mancos	F		X	
1935	Jan 17	UCB 66019	Yuma	Wray	M	X	X	
1935	Dec 6	UCB 70209	Yuma	Wray	M	X	X	
1937	Nov 7	DMNH 3206	Weld	Greasewood	—			
1939	Sep 16	DMNH 3644	Denver	Denver, 1st and Holly	M		X	
1939	Aug	DMNH 3703	Denver	Denver	M			
1940	Aug 21	UCB 95039	Moffat	Craig, 35 km N	M			
1941	Jan	CMNH 19392	Moffat	Morapos Creek, 32 km SW Craig	—		X	X
1941	Oct 16	UCB 96904	La Plata	Durango	—			X
1941	Oct 16	UCB 96905	La Plata	Durango	—			X
1941	Dec 21	CMNH 20627	Moffat	Craig, 8 km W	M		X	X
1942	Jan	CMNH 20628	Moffat	Craig	F		X	X
1943	Apr 18	DMNH 5199	Chaffee	Buena Vista	M		X	
1946	Feb 10	AMNH 140397	Costilla	Ft. Garland–Buck Mountain	M	X	X	X
1951–52	Winter	Destroyed	Bent	Las Animas	—			
1952	Sep	Destroyed	Weld	Dearfield, 8 km E	—			
found 1977		CDOW 230	Logan	T10N R45W S21	—		X	
KANSAS								
ca 1877	—	Unknown	Wallace	Ft. Wallace	—			
1883	Nov 20	CU 4971	Trego	—	—			X
1884	Oct 10	USNM 188450	Trego	—	M		X	X

Other	Collecter	Citation	Measured by us	Remarks
			X	Gunnison's prairie dogs
X-mount	W. S. Carlos (A. M. Alexander)			Gunnison's prairie dogs
	O. Wright (A. M. Alexander)			Gunnison's prairie dogs
				Gunnison's prairie dogs
X-mount	Mrs. M. H. Maxwell	Coues 1877		
	Dr. Law (through F. V. Hayden)	Coues 1877		
	S. N. Rhoads		X	
	C. K. Worthan (donated by S. N. Rhoads)			
				White-tailed prairie dogs
	C. E. Aiken			
X	C. E. Aiken	Cary 1911		
	E. R. Warren		X	2,806 m elevation; Gunnison's prairie dogs
	E. R. Warren		X	
	G. DeLong		X	3,126 m elevation; dead in lake (origin unk.)
		Warren 1910	X	White-tailed prairie dogs
X	R. S. Bull	Felger 1910; Warren 1910		R. S. Bull Collection, Meeker Hotel; white-tailed prairie dogs
X	R. S. Bull	Felger 1910; Warren 1910		R. S. Bull Collection, Meeker Hotel; white-tailed prairie dogs
	E. R. Warren			
X	C. Deardorff		X	Standing mount
	E. Sutton		X	
	W. W. Davidson		X	
X	W. W. Davidson		X	Standing mount
	J. B. Burns		X	
	W. D. Hollister		X	
	A. H. Burns		X	
	A. H. Burns		X	
			X	Gunnison's prairie dogs
	R. J. Niedrach		X	
	S. O. Singer		X	
	S. O. Singer		X	
	S. O. Singer		X	
			X	Gunnison's prairie dogs
	S. O. Singer			
	D. Spencer			
	O. W. Shirley		X	Gunnison's prairie dogs
	O. W. Shirley			
	R. Dietrich		X	Road kill
				Road kill
	A. E. Borell			White-tailed prairie dogs
	W. Dicus			White-tailed prairie dogs
	F. Barnes			Gunnison's prairie dogs
	F. Barnes			Gunnison's prairie dogs
	W. Dicus			White-tailed prairie dogs
	W. Dicus			White-tailed prairie dogs
	R. C. Prater		X	Gunnison's prairie dogs
	L. E. Miller		X	Gunnison's prairie dogs
		Cahalane 1954		Drowned in ditch.
		Cahalane 1954		Road kill
		Bissel 1979		
X-mount	L. H. Kerrick	Coues 1877		
				Not listed in Choate et al. 1982.
	A. B. Baker		X	

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skeleton	Crania	Skin
1885	Oct 20	USNM 15471/22427	Trego	—	F		X	X
1886	Apr 3	USNM 15470/22311	Trego	—	M		X	X
1886	Nov 20	USNM 188451	Trego	—	M		X	X
1887	Mar 31	USNM 188452	Trego	—	F		X	X
1887	Apr 3	USNM 188453	Trego	—	M		X	X
1887	Apr 5	USNM 188454	Trego	—	M			X
1887	Apr 5	USNM 188455	Trego	—	M		X	X
1887	Oct 17	AMNH 1203/1928	Trego	—	M		X	X
ca 1888	—	USNM 12299/22929	Wallace	Ft. Wallace	(M)		X	X
1888	—	USNM 188458	Trego	—	M	X	X	
1889	Apr 15	USNM 188456	Trego	—	F		X	X
1889	Apr	USNM 188457	Trego	—	F		X	X
1889	Nov	USNM 22537/30064	Trego	—	F		X	X
1890	May 8	USNM 22538/30065	Gove	—	M		X	X
1890	June 2	USNM 22539/30066	Gove	—	M		X	X
1891	Jan	USNM 25358/32771	Trego	Banner	F		X	X
1891	Feb 7	USNM 83992	Trego	Banner	M		X	
1891	Feb 4	USNM 83994	Trego	Banner	M		X	
ca 1891	—	USNM 19262/35376	Trego	—	M		X	X
ca 1891	—	USNM 19263/35016	Trego	—	M		X	X
1891	—	USNM 19294/35017	Trego	—	M		X	X
1891	—	USNM 19295/35018	Trego	—	M		X	X
1891	—	USNM 34977	Trego	—	M		X	X
1891	—	USNM 35011	Trego	—	F	X	X	X
1891	Mar 6	USNM 83993	Trego	Banner	F		X	X
1891	—	USNM 19538	Trego	—	M			X
1896	Nov 24	KUMNH 1487	Kingman	Kingman	M		X	X
1901	Nov 2	USNM 110772	Logan	Oakley	M		X	
1904	Dec	UCM 895	Saline	—	M			
1905	—	MCZ 42723	Trego	Wakeeney	(M)		X	X
1909	—	to USNM (no record) (NZP 7494)	Wallace	—	F			
1910	—	USNM 199737 (NZP 7802)	Wallace	—	F		X	
1910	—	Destroyed (NZP 7804)	Wallace	—	—			
1910	—	Unknown (NZP 7803)	Wallace	—	—			
1910	—	London Zoo (NZP 7805)	Wallace	—	—			
1914	May	SDNHM 6720	Decator	—	F			X
1914	Sep	KUMNH 134415	Trego	Banner	M		X	X
1930	Fall	KUMNH 10177	Lincoln	Lucas	M		X	X
1933	Oct	KUMNH 11077	Hamilton	Coolidge	M	X	X	X
1935	Jan 24	MCZ 43727-KU 10973	Hamilton	Coolidge	M	X	X	
1935	Jan	KUMNH 12119	Hamilton	Coolidge	M	X	X	X
1939	—	CM 21391	Jewell	Ionia	M			
1944	Oct	HM 25099	Smith	S of Invale, Neb.	M			
1957	Dec 31	KSU	Sheridan	Studley	M		X	X
found 1978	—	MHP 15569	Gove	Healey, 13 km NW	—		X	
MONTANA								
ca 1877	—	Unknown	—	"Milk River"	—			X
1892	Aug	ANSP 8041	Cascade	Great Falls	F		X	
1910	Jan	USNM 155475	Dawson	Glendive	(M)		X	X
1915	—	SCZ MUNICH	Garfield	Jordan	M		X	
1915	—	FMNH 25621	Garfield	Jordan	—	X		
1915	—	FMNH 25622	Garfield	Jordan	M	X		
1915	—	FMNH 25623	Garfield	Jordan	—		X	
1916	May	MSU 369	Custer	—	M	X	X	
1916	Sep 23	UCB 25709	Garfield	Jordan, 6 km S	M	X	X	X
1916	Sep	USNM 224450	Custer	Kimball	M		X	X
1916	Sep 23	AMNH 40078	Garfield	Jordan, 6 km S	M		X	
1919	May	USNM 232400	Rosebud	NW Calabar, Whitetail Creek	M		X	X
1920	Jan	USNM 239138	Teton	Choteau	(M)		X	X
1920	Apr	USNM 234970	Powder River	Broadus	F		X	X
1920	Apr	USNM 234971	Powder River	Broadus	F		X	X

Other	Collecter	Citation	Measured by us	Remarks
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	L. H. Kerrick		X	NZP specimen; (no accession card) from NZP to USNM 22 May
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	
	A. B. Baker		X	BSC
	A. B. Baker		X	BSC
	C. A. Hawkes		X	
	L. W. Purington		X	
	L. W. Purington		X	
			X	NZP (no accession card), rec'd. 19 Feb by USNM
			X	NZP (no accession card), rec'd. 19 Feb by USNM
			X	NZP (no accession card), rec'd. 24 Feb by USNM
			X	NZP (no accession card), rec'd. 24 Feb by USNM
			X	NZP (no accession card), rec'd. 19 Feb by USNM
			X	NZP (no accession card), rec'd. 19 Feb by USNM
	L. W. Purington		X	
	A. B. Baker		X	
	W. H. Osgood		X	BSC
X-mount	E. H. Herrick (L. H. Kerrick?)		X	NZP rec'd. 3 Apr 1909; died Nov 2 1911
	H. Byxbe		X	NZP rec'd. 17 Jun 1910; died 2 Jul 1915
				NZP rec'd. 17 Jun 1910; died 26 Nov 1913
				NZP rec'd. 17 Jun 1910
				NZP rec'd. 17 June 1910; exchanged 2 Feb 1911
	R. Kellogg		X	
	O. Conrad		X	
	D. Conard (O. Conrad?)		X	Permanent loan to MCZ 4 Jan 1949
				Missing
X-mount		Choate and Fleharty 1975		"Iona"; body mount
	C. Karnes	Taylor 1961 Boggess et al. 1980		
	C. Cavilieer	Coues 1877		
	R. Williams (donated by S. N. Rhoads)			
X-mandible	L. L. Walters	P. Youngman, pers. comm.	X	From FMNH
	Parker & Wells			Skin missing Apr 1980
	L. L. Walters		X	
			X	
	L. L. Walters		X	ADC Reports
			X	
			X	
			X	

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skeleton	Cranium	Skin
1920	May	USNM 234972	Powder River	Broadus	F		X	X
1920	May	USNM 234973	Powder River	Broadus	M		X	X
1920	Oct	Unknown	Rosebud	Ashland	—			
1923	Sep	USNM 243818	Rosebud	Birney	M		X	X
1923	Sep	USNM 243819	Rosebud	Birney	F		X	X
1923	Oct	USNM 243820	Powder River	Ashland, E	F		X	X
1923	Nov	Unknown	Rosebud	Lee	—			
1923	Nov	USNM 243909	Bighorn	St. Xavier	F		X	X
1923	Nov	USNM 243910	Bighorn	St. Xavier	(M)		X	X
1923	Nov	Unknown	Rosebud	Ashland	—			
1923	Nov	Unknown	Rosebud	Ashland	—			
rec'd 1923		USNM X 23272	Bighorn	Crow Agency	—			X
1923	Dec	Unknown	Powder River	Camps Pass	—			
1923	Dec	Unknown	Phillips	Phillips	—			
1924	Jan	Unknown	Phillips	Regina	—			
1924	Sep	Unknown	Choteau	Geraldine	—			
1928	Aug	Unknown	Prairie	Terry	—			
1928	Aug	Unknown	Prairie	Terry	—			
1935	Sep	UCB 78134	Carter	—	M	X		
1942	Jan	USNM 288288	Fergus	Harlowtown, 48 km N	—			X
1944	Oct	KU 14411	Carter	—	M	X	X	X
1948	Sep	Destroyed	Golden Valley	Lavina, 8 km S	M			
1949	Mar	MSU 370	Yellowstone	Billings, 16 km SE	M		X	X
1952	—	Unknown	Rosebud	Ingomar	M		X	
1953	Nov	USNM 287322	Carter	Alzada, 11 km N	M			X
found 1983		BSC	Blaine	Ft. Belknap Reservation T30N R25E S17	—		X	
found 1984	Jan	MDFWP 2344	Carter	Ekalaka	(M)			
found 1984	Jan	MDFWP	Carter	Ekalaka	—			
—	—	USNM 13113/21976	Bighorn	Ft. Custer	(M)		X	X
NEBRASKA								
ca 1877	—	USNM 14580	—	—	(M)	X	X	
1890s	—	Private Collection	Frontier	Curtis	—			
1890s	—	Private Collection	Frontier	Curtis	—			
1890s	—	Unknown	Lancaster	Lincoln	—			
ca 1890s	—	UNZM 2333	Box Butte	Marsland, 8 km SE	—		X	
1917	Sep	AMNH 42567	Sioux	Agate	M		X	
1919	May	Brookings 1989	Frontier	Maywood	—			
1927	—	HM 10038a	Buffalo	Gibbon	—			
1934	Mar 10	AMNH 121610	Webster	Rosemont	M		X	X
1938	Jan 26	HM 18041	Clay	Glenvil	—			
1938	—	Unknown	Custer	Anselmo	F			
1939	Apr 16	HM 19074	Furnas	Cambridge	—			
1946	May 6	UNZM 3323	Banner	Gering, 14 km S	F			X
1947	—	Destroyed	Knox	—	—			
1949	Mar 16	NGFP	Phelps	Overton, S. Platte River	—			
—	—	Private Collection	Garden	Oshkosh	—			
—	—	Brookings 10038b	Buffalo	Gibbon	—			
—	—	Unknown	Buffalo	Kearney	—			
—	—	Unknown Private Coll.	Hamilton	Harvard, N	—			
—	—	Private Collection	Buffalo	Kearney	—			
—	—	Unknown	Custer	Arnold	—			
—	—	USNM 12387	Lincoln	N Platte			X	
—	—	USNM 12409	Dawes	Spotted Tail Agency				X
NEW MEXICO								
found 1899	Jun	USNM	Chaves	Roswell	—			
1915	Mar 18	YPM 1969	Catron	Reserve, 24 km N	M		X	X
1918	May 1	USNM 228789	McKinley	San Mateo, 16 km NE	M		X	X
1918	Oct 25	USNM 231363	Cibola	Bluewater, 3 km N	M			X

Other	Collecter	Citation	Measured by us	Remarks
			X	ADC Reports
			X	
		D. L. Flath, pers. comm.		ADC Reports
			X	
			X	
			X	
		D. L. Flath, pers. comm.		ADC Reports
			X	
			X	
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
		D. L. Flath, pers. comm.		ADC Reports
	M. W. Jellison			
			X	
	Crabb & Watson	Crabb & Watson 1950		Road kill
	Crabb & Watson	Cahalane 1954 (#10)		
X-baculum		Hoffman et al. 1969:597		
	C. Knowles			
	S. Forrest			
X-mandible	T. M. Campbell III			
			X	
		Coues 1877	X	
		Fichter & Jones 1953 (#4)		Rees Heaton Collection; present disposition unk.
		Fichter & Jones 1953 (#4)		Rees Heaton Collection; present disposition unk.
	L. Bruner	Fichter & Jones 1953 (#1)		
X		Fichter & Jones 1953 (#3)		
	A. Thompson		X	
	C. J. Pfeifer	Fichter & Jones 1953 (#9)		To HM; to Hastings College; present disposition unknown
X-mount	J. Shields	Fichter & Jones 1953 (#10)		
	H. Turner	Fichter & Jones 1953 (#14)	X	
	Stahnke	Fichter & Jones 1953 (#11)		To HM; to Hastings College; present disposition unknown
X-mount		Velich 1961		
		Fichter & Jones 1953 (#13)		To HM; to Hastings College; present disposition unknown
		Fichter & Jones 1953 (#17)		
	R. Block	R. Block, pers. comm.		Trapped
X-mount		Fichter & Jones 1953 (#18)		Road kill
	M. Maryott	Fichter & Jones 1953 (#15)		
		Fichter & Jones 1953 (#12)		To HM; to Hastings College; present disposition unknown
		Fichter & Jones 1953 (#5)		
	W. Townsley	Fichter & Jones 1953 (#6)		
	O. Blevins	Fichter & Jones 1953 (#7)		Kearney Public School
		Fichter & Jones 1953 (#16)		
		Fichter & Jones 1953 (#2)		
X-mandible	V. Bailey (BSC)	Bailey 1932		Formerly confused as Santa Rosa, Guadalupe Co., 1903, now believed to be misstated and is Roswell; BSC
	J. S. Ligon (BSC)			Gunnison's prairie dogs; skin measured
	J. S. Ligon (BSC)		X	Gunnison's prairie dogs
	C. P. Musgrave (BSC)			Gunnison's prairie dogs

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skeleton	Crania	Skin
1918	Mar 22	USNM 230773	Catron	Magdalena, 75 mi SW	F			X
1925	Nov 14	YPM 1970	Bernallio	Albuquerque, 12th St.	M			X
1929	Apr 7	ANSP 14509	Lincoln	Picacho, 5 km S	M		X	X
1929	Dec 8	BSC 1210	Colfax	Moreno Valley, Aqua Fria	F		X	
1930	Aug 13	KU 7146	Santa Fe	Santa Fe, 13 km SW	M	X	X	X
1934	Oct 20	USNM 251453	McKinley	Gallup	(F)		X	X
1937	—	Unknown	Cibola	El Moro National Monument	—			X
1940	—	Unknown	McKinley	Mexican Springs	—			
1954	—	Destroyed	Lea	Lovington, 17 km N	—			
NORTH DAKOTA								
1912	—	Unknown	Morton	Ft. Rice	—			
1913	Jun 20	USNM 201945	Dunn	Quinion between Killdeer & Medora	F		X	
1915	—	Unknown	Mercer	Stanton				
1927	Aug	NDSHS 4173	Golden Valley	Beach	—			
1933	Winter	NDSHS 5159	Slope	Marmarth	—			
1951	Mar 5	NDSHS	Hettinger	Mott, 2 km S	—			
1954	—	NDSHS 13063	—	—	F			
1954	Dec	UM 103451	Sioux	Morristown, S. Dak., 10 km N	M		X	X
found 1980		UND	Billings	SE	—		X	
OKLAHOMA								
1923	Sep	USNM 243787	Cimarron	—	—		X	
1924	Jul	OKSU 9266	Texas	Adams, 13 km SE	F			
1928	Jul 25	OU 2211	Cleveland	Norman, 2 km E	—			X
1932	Winter	Destroyed	Texas	22 km S Kansas line	—		X	
—	—	NSCM 858	Woods	Hopeton	—			
SOUTH DAKOTA								
1889	—	Unknown	Shannon	Pine Ridge Agency	—			X
early 1900s	—	MHM	Pennington	—	M			
early 1900s	—	MHM	Pennington	—	F			
1905	Spring	Unknown	Hand	T109N R70W S26, Bailey	—			
1905	Spring	Unknown	Hand	T109N R70W S26, Bailey	—			
1905	Spring	NYZP-AMNH 22894	Hand	T109N R70W S26, Bailey	M		X	
1905	Spring	NYZP	Hand	T109N R70W S26, Bailey	—			
1905	Winter	Unknown	Bennett	Across line from Merriman, Neb.	—			
1913	—	WHO J23	Pennington	Box Elder	—			
1915	Aug	USNM 209150	Mellette	White River	M			X
1920	Oct 4	Destroyed	Jackson	Interior	M			
1921	Feb	Destroyed	Pennington	Scenic	M			
1922	Mar	Unknown	Custer	Wind Cave National Park	—			
1923	Sep 16	USNM 243799	Shannon	Pine Ridge	(F)		X	X
1923	Nov 1	USNM 243990	Harding	Govert	M		X	X
1924	—	Unknown (n = 3)	—	—	—			
1924	Sep	Unknown	—	—	—			
1924	Oct	Unknown (n = 6)	—	—	—			
1925	—	Unknown (n = 6)	—	—	—			
1925	Mar	Unknown (n = 2)	—	—	—			
1925	Jul	Unknown	—	—	—			
1925	Aug	Unknown	—	—	—			
1925	Sep	Unknown	—	—	—			
1925	Nov	USNM 241014	Shannon	Pine Ridge	F		X	
1925	Dec 24	AMNH 70590	Pennington	Scenic	M	X	X	
1926	—	Unknown	—	—	—			
1927	—	Unknown (n = 2)	—	—	—			
1927	Mar	Unknown (n = 2)	—	—	—			
1927	Apr	Unknown (n = 2)	—	—	—			

Other	Collecter	Citation	Measured by us	Remarks
	J. S. Felkner			Gunnison's prairie dogs
	J. S. Ligon (BSC)			Gunnison's prairie dogs; skin measured
	W. Huber			Skin measured
	Aldous (BSC)	Aldous 1940	X	Skin measured; Gunnison's prairie dogs; kept captive 5 months
	T. E. White		X	Skin measured; Gunnison's prairie dogs
	M. E. Musgrave (BSC)		X	Gunnison's prairie dogs
	J. Brewer	Fortenbery 1971; "probable" Hubbard & Schmidt 1984		Skin made but lost; drowned in pools; Gunnison's prairie dogs
X	W. E. Fair	Halloran 1964; "highly probable" Hubbard & Schmidt 1984		Road kill; fluid specimen made but lost
X-mount	J. Richardson	"probable" Hubbard & Schmidt 1984		Mount made but subsequently destroyed
	H. Eaton	Bailey 1926		To Ag College, Fargo
	S. G. Jewett		X	BSC
X-mount	Kellogg	Bailey 1926		
X-mount	H. L. Rice			
X-mount	J. H. Cramer			Received 13 Jun 1935
X-mount				
X-mount				
X	A. Freidt			
	R. Crooke			
X-mount				
	F. Barkley			
		Hibbard 1934		
X-mount				
	A. B. Baker	Henderson et al. 1969 (#1)		ADC records
X-mount	H. Behrens			H. Behrens Collection
X-mount	H. Behrens			H. Behrens Collection
X-mount		Moon 1905; Henderson et al. 1969 (#6)		
X-mount		Henderson et al. 1969 (#6)		
		Henderson et al. 1969		Sold alive
		Henderson et al. 1969 (#6)		Sold alive; probably sold to NYZP, rec'd 2 BFFs Oct 1905; further at least one of these became AMNH 22894, 1 Jun 1906
X-mount		Henderson et al. 1969 (#7)		ADC records, trapped.
X-mount		Henderson et al. 1969 (#10)		
	R. A. Ward			
	B. Darymple	Henderson et al. 1969 (#13)		ADC records, trapped
	B. Darymple	Henderson et al. 1969 (#14)		ADC records, trapped
		Lovaas 1973		Trapped by ADC and killed
	D. P. Stearns	Linder et al. 1972	X	Captured by D. P. Stearns, BSC, Sep 1923 (Linder et al. 1972); to NZP (cat 11.281) 19 Sep; died 4 Nov 1925; to USNM
	L. Knowles			
		Linder et al. 1972		
		Linder et al. 1972		Trapped ADC
		Linder et al. 1972		Trapped ADC
		Linder et al. 1972		
		Linder et al. 1972		Poisoned
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
			X	
	R. E. Lemley		X	
		Linder et al. 1972		
		Linder et al. 1972		
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skeleton	Crania	Skin
1927	Aug	Unknown	—	—	—			
1927	Sep	AUG	Pennington	Rapid City, 29 km S	F			
1927	Winter	WHO J155	Pennington	Conata	—			
1928	Feb	Unknown	—	—	—			
1928	Mar	Unknown (n = 5)	—	—	—			
1928	May	Unknown	—	—	—			
1928	Aug 13	SDNHM 17538	—	—	F			X
1928	Aug 13	SDNHM 17539	—	—	M			X
1928	Aug 13	SDNHM 17540	—	—	M		X	X
1929	May 10	SDNHM 17537	—	—	M			X
1931	Dec 31	UNZM 4451	Custer	Hermosa	M		X	X
1946	Nov	ISU 33434	Lyman	—	M			X
1950	Dec 8	USNM 285877	Dewey	Isabel, 19 km S	M		X	
1952	Oct 23	UMMNH 3667	Perkins	Zeona, N	F	X		
1953	Dec	USNM 287371	Pennington	Conata Basin	F	X	X	X
1953	Aug	USNM (no record)	Haakon	T1N R24E	F			
1953	Aug	Unknown	Haakon	T1N R24E	M			
1953	Aug	Released WCNP	Haakon	T1N R24E	M			
1953	Aug	Released WCNP	Haakon	T1N R24E	M			
1953	Aug	Released WCNP	Haakon	T1N R24E	F			
1954	Mar	Unknown	Stanley	Midland, 24 km N	M			
1956	Summer	Private Collection	Lake	Madison	—			X
1958	Jan	Private Collection	Ziebach	Faith, 8 km SE	M			X
1958	Summer	Destroyed	Lyman	Reliance, 3 km W	M			
1959	—	Destroyed	Mellette	White River, 16 km S	M			
1959	Fall	SDGFP	Sully	Agar, 19 km W	M			
1960	Summer	DMNH	Washabaugh	T41N R35W	M			
1960	Oct 22	USNM 348132	Sully	Onida, 14 km W	M			
1961	Aug	SDSU 110	Lyman	Reliance, 5 km N	M			
1963	Dec	Destroyed	Mellette	T40N R30W, 24 km SW White River	—			
1964	Sep	SDSU 149	Tripp	T40N R78W	—			X
1964	Oct 7	BNP	Washabaugh	T41N R37W, Wanblee	M			
1965	Aug	SDSU 186	Mellette	T40N R32W	M		X	
1965	Sep 29	SDSU 187	Haakon	T2N R19E	F			X
1965	Oct 10	SDSU 190	Jackson	T2S R20E, 14 km W Kadoka	M			X
1966	Sep	USNM 289498	Mellette	White River	F		X	
1966	Mar	KUMNH 121795	Todd	T38N R26W	M	X		
1967	Apr 29	SDSU 212	Bennett	T37N R39W	F		X	
1967	May 16	SDSU 215	Jones	T3S R29E	F		X	
1967	Sep 12	SDSU 224	Mellette	White River, 5 km W	M			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	PAT	Mellette	—	F			
1971	Fall	Private Collection	Mellette	—	M			
1971	Fall	PAT	Mellette	—	M			
1972		PAT	Mellette	—	F			
1973		PAT	Mellette	—	M			
1973		PAT	Mellette	—	F			
—	—	USNM 122620	Hughes	Pierre	(M)		X	
TEXAS								
1882	—	Unknown	Taylor	Abilene	—			
1885		USNM 15018	Cooke	Gainesville	—			X
1886	—	ROM 19-11-1-47	—	Rio Grande	—		X	X
1886	—	USNM 188459	Cooke	—	M			X
found 1894	May	USNM 65061	Childress	Childress	(M)		X	
1901	—	ANSP 11842	Baylor	Seymour	F		X	X
prior to 1902		Destroyed	Crane	Grand Falls				
1902	Summer	Unknown	Lipscomb	Lipscomb	—			X
1905	—	ANSP 12143	Baylor	Seymour	M			X

Other	Collecter	Citation	Measured by us	Remarks
		Linder et al. 1972		Trapped
X-mount	H. Behrens			
	T. Bennett			
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
		Linder et al. 1972		Trapped
		Linder et al. 1972		ADC capture; specimen in tally from 1928
		Linder et al. 1972		ADC capture; specimen in tally from 1928
		Linder et al. 1972		ADC capture; specimen in tally from 1928
		Linder et al. 1972		ADC capture; specimen in tally from 1929
X	F. M. Dille			
	A. Lester			
	R. Block		X	ADC
X-mount	A. Hinds			
			X	
	G. Barnes	Garst 1954		Carcass frozen to USNM; no record. ADC
	G. Barnes	Garst 1954		Died in captivity, skull only saved. ADC
	G. Barnes	Garst 1954		ADC
	G. Barnes	Garst 1954		Captive until Dec 1953. ADC
	G. Barnes	Garst 1954		
	B. A. Nelson	Henderson et al. 1969 (#56)		
		Henderson et al. 1969 (#68)		
	D. Capp	Henderson et al. 1969 (#82)		
	R. F. Wahlin	Henderson et al. 1969 (#83)		Road kill
	T. Johnson	Henderson et al. 1969 (#90)		Shot
X-mount	O. VonWald			
X-mount	W. Allen	Henderson et al. 1969 (#103)		Through Glen Titus
X-mount	D. Badger & T. Lockwood			
X-mount	C. F. Anderson	Progulske 1969		Died in captivity
		Henderson et al. 1969		R. Adrian observed. Shot
	G. Johnson			Shot
X-mount		Henderson et al. 1969 (#155)		Viscera at SDSU. Shot
	O. Huber			Trapped
	R. Henderson			Killed by ranch dog
	R. Henderson			Road kill
			X	Carcass to SDSU. Shot
	W. Abbot	Henderson et al. 1969 (#196)		Listed in private collection in Henderson et al. 1969. Killed by dogs
X-carcass	J. Milk			Road kill
X-carcass	D. Richardson			Road kill
	J. Krogman			Road kill
X-carcass				Juvenile, died of distemper vaccine
X-carcass				Juvenile, died of distemper vaccine
X-carcass				Juvenile, died of distemper vaccine
X-carcass		Carpenter, pers. comm.		Juvenile, died 1971 of distemper vaccine
X-carcass		Carpenter, pers. comm.		Juvenile, captive 6 years, died 1978; to Meeteetse Bank Apr 1982
X-carcass		Carpenter, pers. comm.		Captured as juvenile, captive 4 years, died 1976
X-carcass		Carpenter, pers. comm.		Captured as juvenile, died Oct 1978
X-carcass		Carpenter, pers. comm.		Adult, died Apr 1979
X-carcass		Carpenter, pers. comm.		Adult, died Jan 1979
			X	
	F. J. Thompson	Coues 1882		Captured live; held at Cincinnati Zoo
	G. H. Ragsdage	True 1885		
			X	
				Captive Philadelphia Zoo 27 Apr 1901–2 Sep 1903; accession to ANSP 5 Jan 1904; Zool. Soc. Philadelphia
		Bailey 1905		
		Bailey 1905		
				Zool. Soc. Phila., received 14 Aug 1905, died 27 Nov 1905; accession ANSP 1905

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skeleton	Crania	Skin
1905	—	Private Collection	Baylor	Seymour	F			
1933	Dec	UCM 5263	Lubbock	Lubbock	M		X	
1934	Feb	UCM 5287	Lubbock	Lubbock	M		X	
1934	Dec 21	UM 76971	Lubbock	Slide, 5 km SW	M		X	X
UTAH								
1937	Apr 21	UCB 77840	San Juan	Blanding, 3 km S	M			
WYOMING								
1851	—	USNM	Goshen	Ft. Laramie	—			X
ca 1877		Unknown	Laramie	Cheyenne Depot	—			
1883	Dec	USNM 13996/21066	Laramie	Cheyenne, 19 km on Duck Creek	—		X	
1895	May	USNM 71750	Weston	Newcastle	F			X
1910	May	USNM 168741	Weston	Newcastle	(M)		X	
1911	Spring	USNM 180719	Crook	Beulah	M			X
1911	Oct	USNM 180718	Johnson	Clear Creek, above Big Red (Ucross)	—			X
1916	Apr	USNM 211513	Niobrara	Manville	M		X	
1916–1928		Unknown (n = 10)	—	—	—			
1917	Sep	USNM 227703	Converse	Douglas	M			X
1924	Oct	USNM 245641	Albany	Laramie, 8 km W	M		X	X
ca 1930	—	Private Coll. (n = 2)	Park	—				X
1935		Private Collection	Sheridan	Leiter, 22 km N	M			X
1939	Nov	Private Collection	Albany	Eagle Park, W of Laramie Peak	—			X
ca 1946	—	Unknown	Sweetwater	Wamsutter and Rock Springs	—			X
1950	—	Destroyed	Albany	Laramie, 2 km W	—			
1955	—	UW	Albany	Laramie	—			
1981	Sep 26	BSC 7934	Park	Meeteetse	M	X	X	X
1982	Mar	BSC (Biota #11)	Park	Meeteetse	M	X	X	X
1982	Spring	BSC (Biota #1)	Park	T48N R102W S17	(F)		X	
1982	Winter	BSC 10481	Park	Meeteetse	M	X	X	X
1983	Aug	WGF (Biota #16)	Park	Meeteetse	—	X	X	X
1983	Winter	WGF (Biota #14)	Park	T48N R102W S18	M			
1983	Oct	BSC	Park	T48N R102W S4	F			
1983	Dec	USFWS	Park	T48N R102S S7	M		X	
1984	Winter	WGF	Park	T48N R102W S8	F			
1984	Sep	BSC	Park		M		X	
1984	Sep	BSC	Park		F			
found 1978		BSC	Carbon	T22N R77W S31, S Medicine Bow	(M)		X	
found 1978	Aug 15	BSC 4059	Uinta	T16N R117W S7	(F)		X	
found 1979		WGF	Converse	T41N R70W S32, Rosecrans	—		X	
found 1979		BSC 4442	Unita	T16N R118W S12	(F)		X	
found 1979		BSC 4548	Carbon	T23N R80W S18	(F)		X	
found 1979	Sep 5	BSC 4547	Carbon	T23N R81W S2, 13 km NE Hanna	—		X	
found 1979	Sep 11	BSC 4441	Unita	T16N R118W S1	—		X	
found 1979		BSC 4342	Carbon	T23N R84W S34	(F)		X	
found 1981	Aug 27	BSC 7558	Sweetwater	T22N R93W S33, 19 km N Wamsutter	(F)		X	
found 1982	Spring	BSC (Biota #10)	Park	Meeteetse	(M)	X	X	X
found 1982	Mar 15	BSC (Biota #4)	Park	T48N R102W S8	(F)			
found 1982	Apr 20	BSC (Biota #5)	Park	T48N R102W S7	(M)		X	
found 1982	Apr 23	BSC (Biota #6)	Park	T48N R102W S8	—		X	
found 1982	Jun 9	BSC (Biota #7)	Park	T49N R102W S31	(F)		X	
found 1982	Jun 26	BSC (Biota #9)	Park	T48N R103W S2	(M)		X	
found 1982	Aug 9	BSC (Biota #3)	Park	T48N R102W S7	(F)		X	
found 1982	Sep 22	BSC (Biota #14)	Park	T48N R103W S2	(F)		X	
found 1982	—	WGF	Park	Meeteetse	M	X	X	X
found 1982	—	WGF	Park	Meeteetse	M	X	X	X
found 1983		WGF (Biota #15)	Park	T48N R102W S7	—			
found 1984	Apr 8	BSC	Park	Meeteetse				
found 1984	Spring	WGF	Park	Meeteetse			X	

Other	Collecter	Citation	Measured by us	Remarks
				D. White from ZSP, received 14 Aug 1905, died 28 Feb 1906
	D. Spencer		X	
	D. Spencer		X	
	P. A. Burns			Gunnison's prairie dogs
	A. Culbertson	Audubon & Bachman 1851		Destoyed by 1872 (Coues 1872).
X-mount	Capt. J. Gillis	Coues 1877		
	J. Mason and C. Ruby		X	
	F. Bond			
	S. E. Piper		X	
			X	
	US Biological Survey	Day & Nelson 1928		Killed 10 in predator trapping
				White-tailed prairie dogs
	B. Edgar	Clark 1975		
		Clark 1975		
		Clark 1975		
	P. Muchmore	Clark 1975		Road kill; formerly in WGF collection; white-tailed prairie dogs
	R. W. Fautin			Road kill
	R. W. Fautin			Stolen; white-tailed prairie dogs
	L. Hogg		X	Hogg Ranch kill; white-tailed prairie dogs
	J. Renner			Road kill; white-tailed prairie dogs
	L. Richardson		X	White-tailed prairie dogs
	T. W. Clark		X	Starved in burrow; white-tailed prairie dogs
	T. W. Clark			Juvenile; white-tailed prairie dogs
X-carcass	M. Karl			Young of year; white-tailed prairie dogs
X-carcass	D. E. Biggins		X	Killed by predator; young of year; white-tailed prairie dogs
X-carcass	D. E. Biggins			Adult, killed by predator; white-tailed prairie dogs
X-carcass	J. Hasbrouck			Adult; white-tailed prairie dogs
X-partial cranium	D. E. Biggins			Partial cranium; killed by predator; juvenile; white-tailed prairie dogs
X-mandibles	V. Semonsen			Killed by predator; juvenile; white-tailed prairie dogs
	T. M. Campbell III	Clark and Campbell 1981	X	Adult; white-tailed prairie dogs
		Martin & Schroeder 1978		1/2 skull
	J. Bridges			
	V. Jameson	Martin & Schroeder 1979	X	White-tailed prairie dogs
		Martin & Schroeder 1979	X	White-tailed prairie dogs
	D. Higgins	Martin & Schroeder 1979		1/2 skull; white-tailed prairie dogs
	S. Martin	Martin & Schroeder 1979	X	White-tailed prairie dogs
		Martin & Schroeder 1979	X	White-tailed prairie dogs
	S. Martin		X	White-tailed prairie dogs
	L. Richardson			Full head (eagle); white-tailed prairie dogs
	T. W. Clark		X	Adult; white-tailed prairie dogs
	J. Grenier		X	Adult; white-tailed prairie dogs
X-mandibles	T. W. Clark		X	Subadult; white-tailed prairie dogs
	S. C. Forrest		X	Adult; white-tailed prairie dogs
	L. Richardson		X	Subadult; white-tailed prairie dogs
	L. Richardson		X	Adult; white-tailed prairie dogs
	L. Lee		X	Adult; white-tailed prairie dogs
	T. Thorne			Trap kill; white-tailed prairie dogs
	T. Thorne			Trap kill; white-tailed prairie dogs
X-mandibles	T. W. Clark			White-tailed prairie dogs
	T. Taylor		X	White-tailed prairie dogs
	B. Phillips			White-tailed prairie dogs

TABLE 6 continued.

Year	Date	Disposition	County	Site	Sex	Skeleton	Crania	Skin
SASKATCHEWAN								
1924	Sep 30	SMNH 1588	—	Regina, 6 km SE	M			
1930	Feb	NMC 11693	—	Shaunavon	—			X
1931	Dec 20	SMNH 3183	—	Gergovia, S35 T2 R24	F			X
1932	—	NMC from SMNH 2965	—	Big Beaver, S5 T2 R24	—			X
1932	Dec 1	NMC 11703	—	Frontier	—			X
1932	Dec 21	NMC 11700	—	Shaunavon, 32 km SE	F	X		X
1932	Dec 28	NMC 11752	—	Climax, S33 T3 R18	M	X		X
1933	Jan	NMC 11744	—	Shaunavon	M			X
1933	Jan 6	SMNH 3168	—	Climax	—			X
1933	Apr	SMNH 3186	—	Expanse, 8 km N	—		X	X
1934	Nov 23	NMC 12682	—	Shaunavon	M		X	X
1935	Nov 20	NMC 14078	—	Senate	M		X	X
1935	Nov	NMC 14095	—	Wood Mountain	M	X		X
1935	Dec 5	NMC 14079	—	South Fork, 19 km N	M	X		X
1935	Dec 4	SMNH 3656	—	Keeler, S22 T19 R29	—			
1935	Dec	SMNH 3657	—	Hazlet	—			
1937	Dec 7	NMC 24235	—	Climax, 11 km N	F			X
—	—	ROM 33–5–23–2	—	Maple Creek	F	X		X
—	—	SMNH 11441	—	—	—			X
—	—	SMNH 11442	—	—	—			X
ALBERTA								
1901	May	FMNH 8207	—	Gleichen	F		X	X
ADDITIONAL REPORTS								
1888		AMNH 2546			—		X	
1903		AMNH 22820-NYZ 02699			M	X	X	X
1928		NYZ 02701			—			X
1928		NYZ 02700			—			X
1920s		Syracuse (n = 3)						X
1934		ZSP						
1934		ZSP						
prior to 1862	May	MCZ 14947						
		BSC 4282			(F)		X	
		BSC 4283			M		X	
		USNM 35087			M			
		USNM 35088			M	X		
—		BMS			—			X
		FMNH						X
		AMNH 35041			M	X		
ca 1877		USNM 11932						
MISSOURI								
1876		USNM 21965		Licks's River	(F)		X	

COLORADO

Fifty-four specimens of ferrets are listed from Colorado (Table 6, Fig. 11), including 47 specimens in museums and an additional 7 verified specimens whose present dispositions are unknown. Armstrong (1972) examined 30 specimens from Colorado and listed an additional 27 records, many of which were sight records only.

The earliest known verified specimen is AMNH 24412, collected in 1878 in El Paso County. Coues (1877), however, mentioned several accounts of black-footed ferrets from Colorado and had at least two occasions to examine specimens from there. One was a specimen in "defective" condition shot in "the valley of the Cache La Poudre River, near the northern border of Colorado" (Larimer

Other	Collecter	Citation	Measured by us	Remarks
X-mount				
	C. Pickett			
				Not in collection—missing
	H. F. Hughes			
	H. F. Hughes			
	J. Prochazka			
				Missing
				Missing
	C. Guiguet			
	W. Klym			
	H. F. Hughes			
X-mount				
X-mount				
	F. Nevada			
	C. B. Spangler			
				Partial skull; "out of range."
				NYZ specimen (no acc. card); to AMNH 20 June 1888
				Collected prior to Sep 1903; died Aug 1905; skin to AMNH 5 Aug 1905
				Collected prior to 10 Apr 1928; died 6 Jul 1928; skin to AMNH (no record); gift of William J. Brunner
				Collected prior to 10 Apr 1928; died 8 Jul 1928; skin to AMNH (no record)
				Three specimens; no data, skins
				Received 1 Jun 1934; Urban J. Jones, Laureldale, Penn; died Jan 1939
				Received 1 June 1934, Urban J. Jones, Laureldale, Penn.; died Jan 1939
	F. J. Thompson			In alcohol; lost
			X	No data
			X	No data
			X	National Zoo specimen (no acc. card) to USNM
			X	National Zoo specimen (no acc. card) to USNM; skeleton only
				No data
				No data; probably belongs to skull in SCZ, Munich
				No data
	J. W. Munyon	Coues 1877		Platte River, not in current records
			X	"Out of range."

County) presented to the USNM sometime between 1872 and 1877 by Dr. V. F. Hayden. This specimen is no longer in the USNM collection. Hayden told Coues that another ferret was kept in captivity for some time at Greeley. Coues also examined the collection of the pioneer naturalist Mrs. M. A. Maxwell of Boulder and verified several specimens taken "in the vicinity of Denver" at a centennial exhibition in Washington, D.C., in 1876 (Coues 1877). The disposition of Mrs. Maxwell's collection is unknown. Both Hayden and Maxwell "represented the species as being not at all rare."

The most recent preserved specimen was obtained in Costilla County in 1946. Cahalane (1954) listed one specimen from Weld County in 1952, which was verified but subsequently

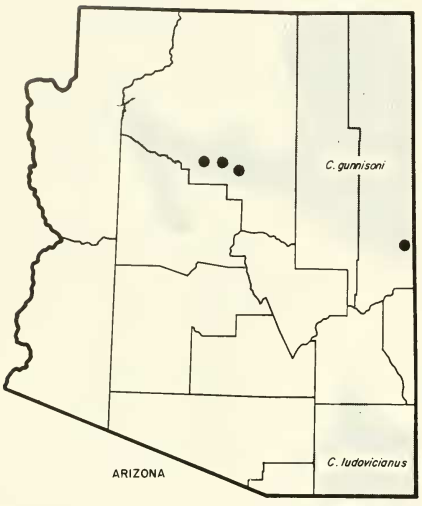

Fig. 10. Black-footed ferret specimens from Arizona. Prairie dog distribution (shaded) after Cockrum (1960).

destroyed. Eight of 10 of the most recent specimens (1940–1952) were collected west of the Front Range. One mandible was found in prairie dog colony searches in Logan County in 1977 (Bissell 1979), but, like many specimens found ejected from burrows by prairie dog digging activity, it may have been underground for an undetermined length of time before being brought to the surface. A record for Sedgewick County listed by Armstrong (1972) was found to be a sight record only and is not listed.

Two specimens were found above 2800 m. One of these (UCM 10658) was found in association with *C. gunnisoni* in Teller County at 2800 m. The other specimen (UCM 10660) was found drowned in Lake Moraine, elevation 3125 m in El Paso County, far from any prairie dog colony. This specimen and another from Grand County (DMNH 653) were the only two specimens from Colorado not directly associated with prairie dogs and may have represented dispersing individuals.

Three species of prairie dogs occur in Colorado: *C. ludovicianus*, *C. leucurus*, and *C. gunnisoni*. Burnett (1918) estimated that the three combined species occupied 5,665,720 ha in the state in 1918. The area now occupied by prairie dogs in the state is unknown, but it is greatly reduced. Gilbert (1977) identified 10,843 ha of *C. leucurus* colonies in Rio Blanco and Moffat counties in 1977 and Bissell (1979) estimated 21,500 ha for 9 of 26 counties in *C. ludovicianus* range in the state in 1978. No estimate of *C. gunnisoni* distribution is available. Over 247,230 ha of *C. gunnisoni*-occupied colonies disappeared from 1945 to 1947 during epizootics of sylvatic plague (Armstrong 1972).

KANSAS

Occurrence of *M. nigripes* in Kansas was reviewed by Choate et al. (1982). We list eight additional records, including one specimen from Decatur County and one specimen in the CU collection dated 1883 (Table 6). Additional literature records include a mounted specimen from Wallace County examined by Coues (1877) supplied by L. H. Kerrick. About 1888 another ferret from Wallace County that had resided in the National Zoological Park was given by Kerrick to the USNM (12299/22929). These are obviously different specimens, but whether Kerrick was associated with NZP or was the collector of the Wallace County animals is unknown. The disposition of several other animals residing at the NZP from 1905 to 1915 is also indicated in Table 6. Forty-eight specimens are known for the state (Fig. 12).

Of 18 ferrets in Table 6 collected from 1877 to 1890, 15 were collected by A. B. Baker. Several museum labels listing Baker as the collecter also indicate the specimen was collected under the auspices of the BSC, but it is not known whether Baker was employed by BSC. Recent specimens include one collected by hand in 1957 in Sheridan County (Taylor 1961) and a skull and mandible of unknown age found on a prairie dog town in Gove County in 1978 (Boggess et al. 1980).

Ferrets and prairie dogs historically occupied most of Kansas west of the Flint Hills (Fig. 12). However, prairie dogs that occupied an estimated 809,390 ha in Kansas in 1903 were reduced to some 14,570 ha (98% reduction) by 1973 (Choate et al. 1982). Choate et al. (1982) feel that ". . . the outlook is poor that the black-footed ferret will continue to occur in Kansas, if, indeed, any remain here now."

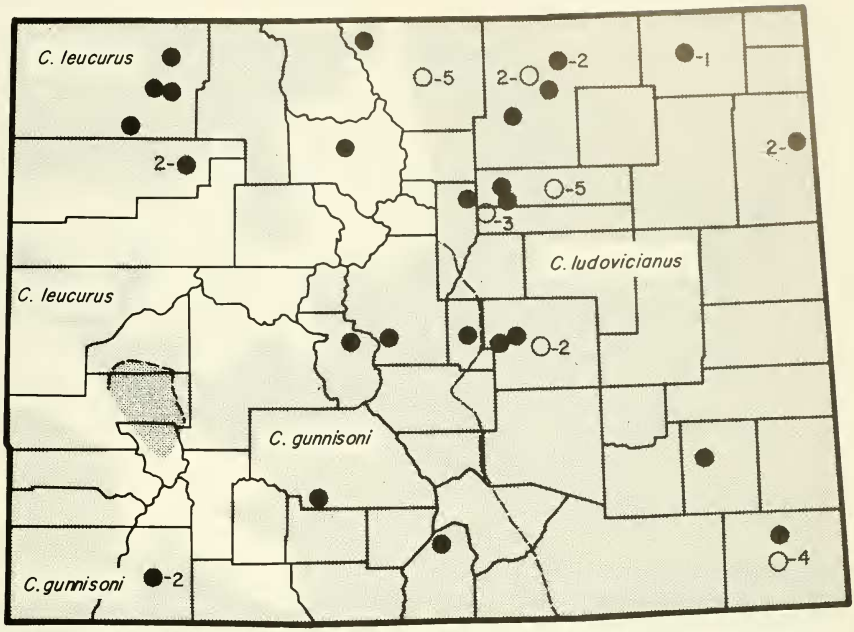

Fig. 11. Black-footed ferret specimens from Colorado. Prairie dog distribution (shaded) after Armstrong (1972).

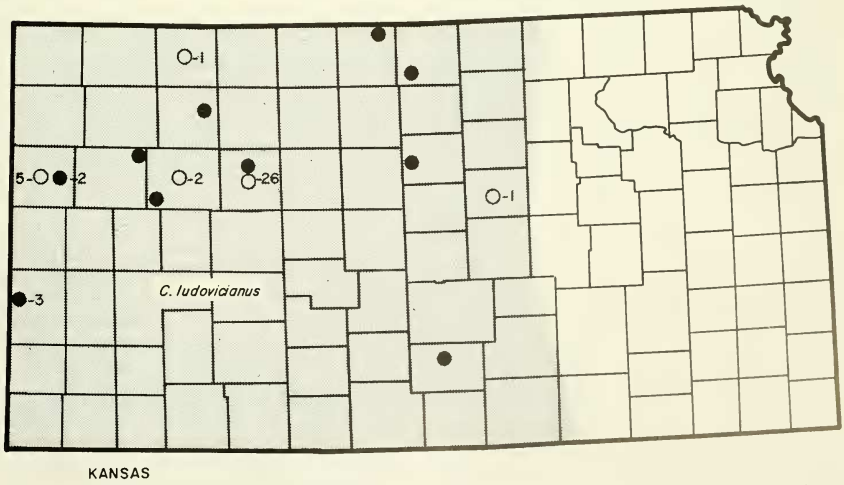

Fig. 12. Black-footed ferret specimens from Kansas. Prairie dog distribution (shaded) after Choate et al. (1982).

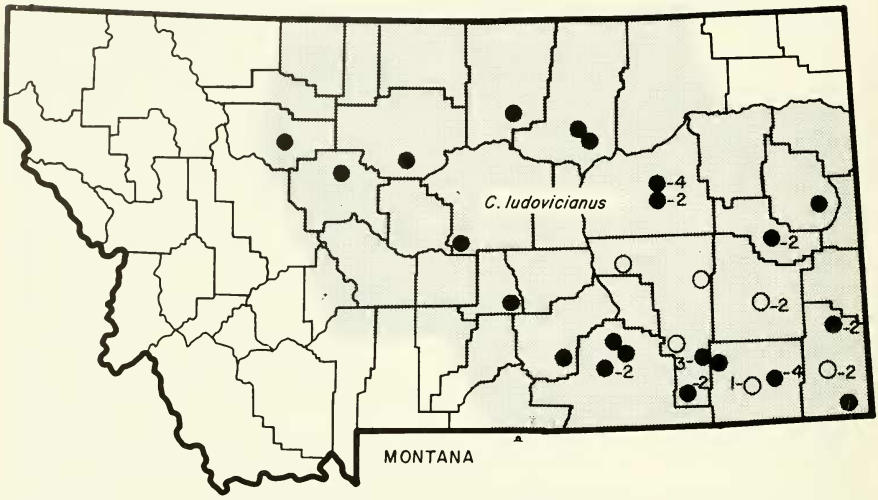

Fig. 13. Black-footed ferret specimens from Montana. Prairie dog distribution (shaded) after Hall (1981).

MONTANA

Specimens of the black-footed ferret from Montana have not been described. Forty-four specimens are known from the state (Table 6, Fig. 13). Coues (1877) reported the earliest specimen (now lost) from the "Milk River." The most recent specimen was taken in Carter County in 1953. Thirty two (73%) of these ferrets come from seven counties in the southeastern part of the state. An undated specimen (USNM 13113/21976) lists the collection location near "Ft. Custer." Ft. Custer (in Bighorn County) was activated in 1877 and decommissioned in 1898, so it is assumed the specimen dates from that period.

Prairie dogs (*C. ludovicianus* except for a small intrusion of *C. leucurus* in southern Carbon County [Flath 1979]), occupy the eastern two-thirds of the state except the three extreme northeast counties (Daniels, Roosevelt, Sheridan) north of the Missouri River (Hall 1981). Historic distribution of prairie dogs in the Burlington Northern Railroad right-of-way showed extensive contiguous areas (Flath and Clark 1986). Federal programs poisoned 2,832,860 ha of prairie dog and ground squirrel habitat in Montana in 1920 alone (Bell 1921). Vigorous prairie dog control efforts continued on a statewide basis until the 1950s, and in some counties areas of prairie dogs were reduced substantially (U.S. Bur. Land Mgmt. 1982). There is no estimate of the current total area occupied by prairie dogs in the state.

In 1984 and T. M. Campbell and SCF found two separate remains, a black-footed ferret skull and a mandible (MDFWP 2344a and 2344b) on a prairie dog colony in Carter County, where ferrets reportedly had been observed in 1977 (Jobman and Anderson 1981). From the condition of the remains and the recent occupancy history by prairie dogs in the area, it was estimated that they were no more than 10 years old, supporting the 1977 sighting. Repeated searches in the area failed to produce other evidence or observations of living animals.

NEBRASKA

Black-footed ferrets from Nebraska were recorded by Fichter and Jones (1953) and Jones (1964). We list an additional six specimens, for a total of 23 from the state (Table 6, Fig. 14). The most recent specimen was a road kill from Dawson County in 1949.

Additional information on two specimens is also available. A specimen mentioned by Coues (1877) and identified (USNM 14580) as coming from Nebraska has no date but should be about the time of the Coues report of 1877.

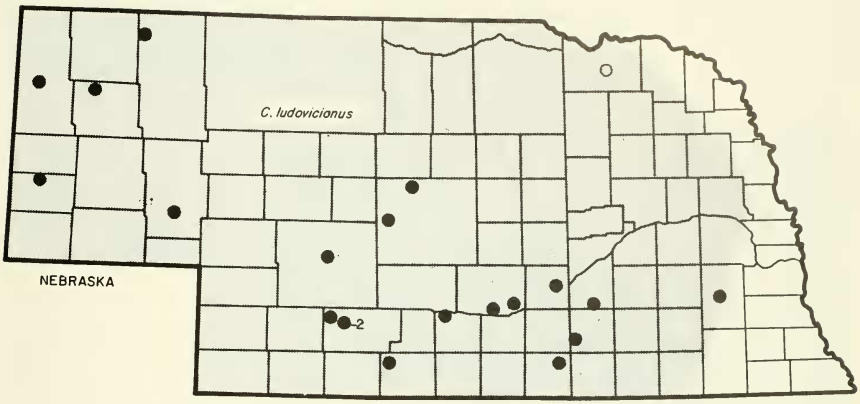

Fig. 14. Black-footed ferret specimens from Nebraska. Prairie dog distribution (shaded) after Jones (1964).

The whereabouts of a second specimen (Fichter and Jones 1953 #10) was unknown, but it is recorded correctly in Jones (1964) as AMNH 121610. We include all of the Fichter and Jones (1953) list except number 8, from Fremont, Dodge County, which was a secondary report.

Prairie dogs (*C. ludovicianus*) probably were restricted historically to the "hard lands" described in Fichter and Jones (1953), which excludes much of the north central Sand Hills region. No estimate of their historic abundance is available, but they probably were found in great numbers along the many tributaries of the Platte and Niobrara rivers. Lock (1973) estimated only 6070 ha of prairie dog colonies remained statewide in 1971.

New Mexico

Status and history of the black-footed ferret in New Mexico are described in detail by Hubbard and Schmitt (1984). We include three records of "unsubstantiated" specimens in our list that are treated separately by them and described as "probable" or "highly probable." Because existence of these specimens is documented elsewhere, we include them here but concur with Hubbard and Schmitt (1984) that some question exists as to their validity. We also agree that a ferret mandible noted in Bailey (1926) as being found in Santa

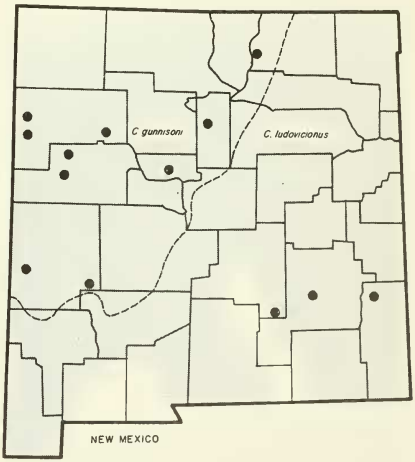

Fig. 15. Black-footed ferret specimens from New Mexico. Prairie dog distribution (shaded) after Hubbard and Schmitt (1984).

Rosa, Guadalupe County, in 1903 is the mandible catalogued in the USNM from Roswell, Chaves County, 1899 by Bailey.

We list 10 extant specimens and three disputed specimens (Table 6, Fig. 15). The last verified specimen was taken in 1934 in

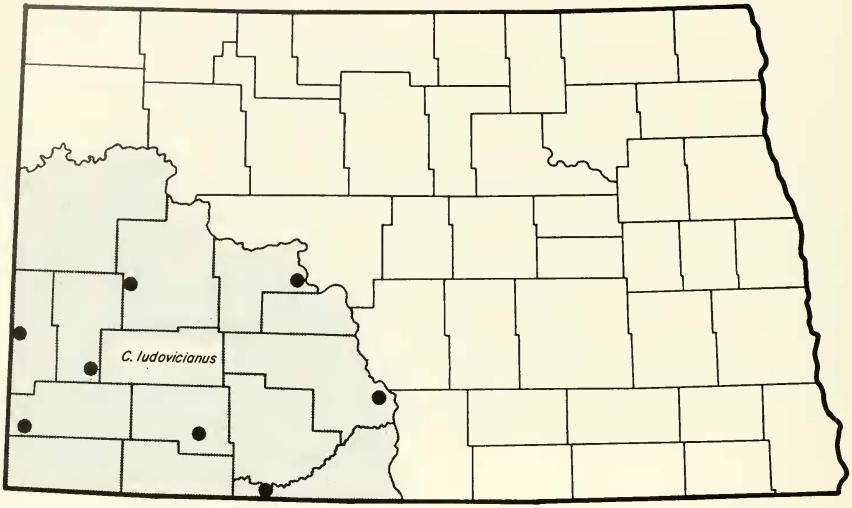

Fig. 16. Black-footed ferret specimens from North Dakota. Prairie dog distribution (shaded) after Hall (1981).

McKinley County. Hubbard and Schmitt (1954) described the substantial role of BSC trappers in the collection of ferret specimens in the state.

Cynomys ludovicianus is found in the southern and eastern parts of the state, and *C. gunnisoni* is found at higher elevations in the northwest. Prairie dog area in the state declined from an estimated 4,856,333 ha in 1919 to less than 202,350 ha in 1979–1981 (Hubbard and Schmitt 1984). Hubbard and Schmitt "assume the ferret is still a member of the state's fauna and that it could occur anywhere that prairie dogs occur."

North Dakota

No account of ferret specimens for North Dakota is available other than Bailey (1926). We located nine specimens, all collected west of the Missouri River (Table 6, Fig. 16). Recent specimens include one found in 1954 in Sioux County and a skull found in 1980 in southeastern Billings County.

Teddy Roosevelt described ferrets found near his ranch in western North Dakota in the late 1800s as "that rather rare weasel-like animal . . . I have known one to fairly depopulate a prairie-dog town, it being the arch-foe of these little rodents" (Seton 1929: 571).

Little is known of former prairie dog (*C. ludovicianus*) distribution, although there were likely prairie dogs found east and north of the Missouri River. In 1920, 2,428,166 ha were treated with poisons for prairie dogs and ground squirrels in North Dakota (Bell 1921). Grondahl (1973) estimated only 2740 ha of prairie dogs remained by 1973, all west of the river. Seabloom et al. (1980:) ". . . regard sightings (of black-footed ferrets) as representing transients rather than a viable resident population" and cite the paucity of prairie dogs remaining in the southwestern part of the state.

Oklahoma

Lewis and Hassein (1973) listed recent ferret specimens and sightings for Oklahoma. Only four specimens are known, with one additional literature reference (Table 6, Fig. 17). A specimen was collected in Cleveland County in 1928, and Hibbard (1934) reported a ferret taken in Texas County in 1932. *Cynomys ludovicianus* probably occupied "millions" of hectares in Oklahoma at the turn of the century, including one colony 35 km long in tall grass prairie between Kingfisher Creek and El Reno (Lewis and Hassein 1973), but only 3845 ha remained in 1968 (Tyler 1968).

Fig. 17. Black-footed ferret specimens from Oklahoma. Prairie dog distribution (shaded) after Hall (1981).

Black-footed ferrets were considered extirpated in Oklahoma as of September 1980 by the U.S. Fish and Wildlife Service, Albuquerque, New Mexico (Jobman and Anderson 1981).

South Dakota

A detailed description of ferret distribution and occurrence is available for South Dakota, where ferrets were studied in Mellette and adjacent counties from 1964 to 1974. Henderson et al. (1969) described ferret specimens and sight reports for South Dakota from 1889 to 1967, and additional records were discussed in Linder et al. 1972. Table 6 includes an additional 15 specimens not in those accounts. Ninety-nine specimens are reported, with 57 specimens destroyed or of unknown disposition (Fig. 18).

Additional notes were also made for the following specimens:

Moon (1905) noted a "pair sold alive" (Henderson et al. 1969: #6). The New York Zoological Park listed two arrivals of *M. nigripes* in October 1905, but no accession card was made to verify this transaction. A specimen that came from NYZP to AMNH (22894) on 1 June 1906 with no data was undoubtedly one of these animals. Disposition of the second animal is unknown. We therefore list AMNH 22894 as coming from this source.

D. P. Stearns, BSC, captured one ferret alive near Pine Ridge, Shannon County, on 16 September 1923. This is undoubtedly the ferret trapped by BSC in Pine Ridge September 1923 reported by Linder et al. (1972). This animal was sent to the NZP (11281), where it lived until 4 November 1925. It was subsequently catalogued into the USNM (243799).

Linder et al. (1972) listed 43 ferrets taken by BSC from 1924 to 1929. Table 6 lists 8 known specimens from that period. Four specimens in the SDMNH were taken in South Dakota during this period and correspond to the 3 specimens taken in 1928 not identified by month in the Linder et al. (1972) list and the 1 specimen from 1929. Therefore we have deducted them from the Linder et al. (1972) tally for those years. The remaining 4 specimens from that period may also have been collected by BSC, but insufficient data are available on the collectors to verify this. Both tallies are therefore included.

Rose (1973) briefly discussed the history of prairie dogs in South Dakota. Towns 24–32 km long were common in major drainages. H. R. Wells estimated 710,935 ha of prairie dogs in the state in 1923 (Linder et al. 1972). In 1968 BSFW estimated 24,281 ha in the state, a reduction of 96% (Rose 1973). Linder et al. (1972) presented data showing 405,000 ha were poisoned by various government agen-

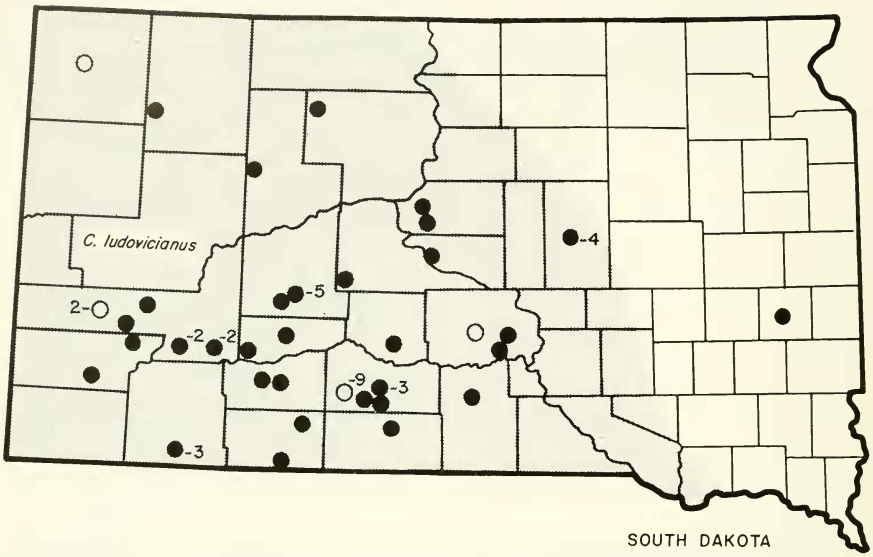

Fig. 18. Black-footed ferret specimens from South Dakota. Prairie dog distribution (shaded) after Hall (1981).

cies between 1932 and 1939. Three counties within the Pine Ridge Indian Reservation (Shannon, Jackson, Bennet) had recovered prairie dog populations occupying in excess of 120,000 ha in 1984 (R. Crete, personal communication).

TEXAS

The distribution of ferrets in Texas has not been described. We have established 13 verified records for the state and have located nine extant specimens (Table 6, Fig. 19). Specimen USNM 15018 is similar in all respects to a specimen described by True (1895) and is listed as such. Four specimens were taken for zoos. Two specimens from Gainesville are slightly out of current range, but may have been within historic range, or Gainesville may have been chosen by the collecter as the nearest identifiable landmark. The occurrence of ferrets in trans-Pecos Texas has been questioned (Schmidly 1977), even though it is highly likely they occurred there. None of these specimens expand the known range in the state.

Bailey (1905) estimated that prairie dogs (*C. ludovicianus*) occupied 233,100 sq km and

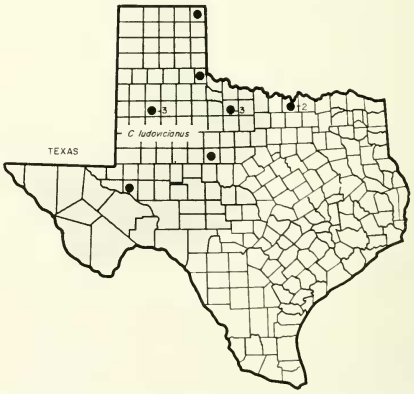

Fig. 19. Black-footed ferret specimens from Texas. Prairie dog distribution (shaded) after Cheatheam (1977).

noted one town in the Panhandle of 6,475,111 ha (400 x 160 km). A statewide survey in 1976 showed 36,432 ha of prairie dogs, which were nowhere in great density (Cheatheam 1977). The U.S. Fish and Wildlife Service, Albuquerque, New Mexico, considers the black-footed ferret extirpated in Texas (Jobman and Anderson 1981).

Fig. 20. Black-footed ferret specimens from Utah. Prairie dog distribution (shaded) after Durrant (1952).

Utah

Only one specimen is known for Utah (Durrant 1952), found in 1937 south of Blanding, San Juan County (Table 6, Fig. 20). Three species of prairie dogs are found in Utah: *C. leucurus*, *C. gunnisoni*, and the endemic Utah prairie dog, *C. parvidens*. *Cynomys parvidens* is geographically disjunct and there is no evidence to suggest that *M. nigripes* has ever occurred with this species.

Wyoming

Black-footed ferret reports from Wyoming have been discussed in Clark (1980) and Clark and Campbell (1981), including an additional 126 sight records not listed here. In all, 60 ferret remains are known from 1851 to 1984, and 24 of these come from the Meeteetse area where the known population is currently under study (Table 6, Fig. 21). Five ferrets listed in Clark and Campbell (1981) were actually from South Dakota (Garst 1954). Ferrets

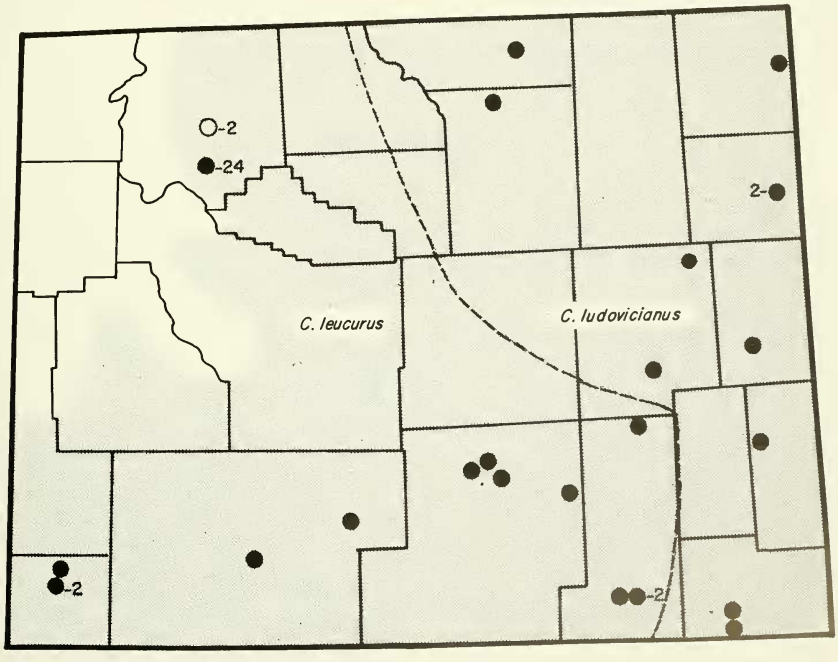

Fig. 21. Black-footed ferret specimens from Wyoming. Prairie dog distribution (shaded) after T. W. Clark, personal communication.

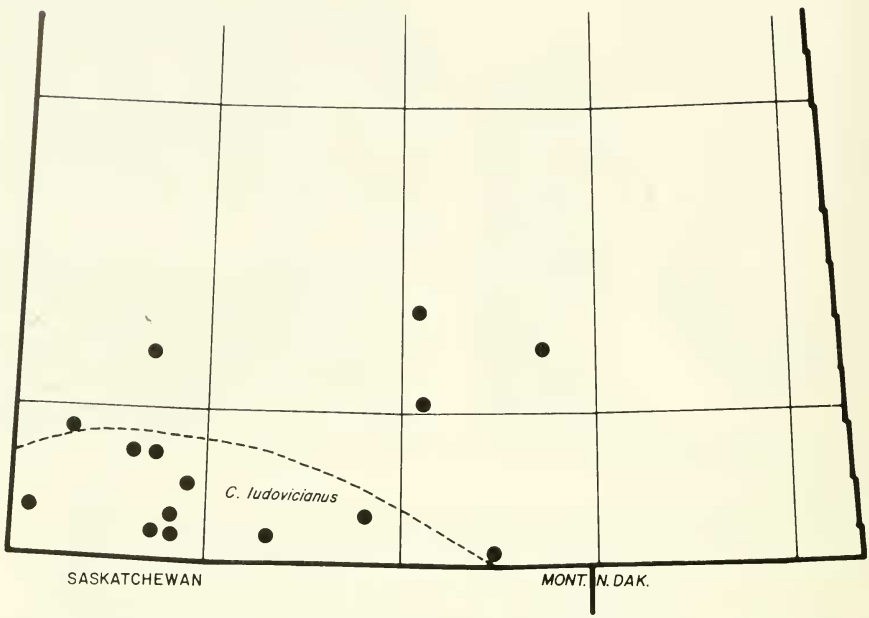

Fig. 22. Black-footed ferret specimens from Saskatchewan. Estimated extent of prairie dogs shown by dotted line.

range farther west in the state than previously reported by Hall (1981).

Ferrets occurred throughout Wyoming, except the mountainous northwestern corner, in association with *C. ludovicianus* in the east and *C. leucurus* in the west. Between 1915 and 1923, 1,120,290 ha were poisoned for prairie dogs (Martley 1954). An additional 445,080 ha were poisoned from 1923 to 1928 in Niobrara, Weston, and Campbell counties only, including one colony 160 km long from Indian Creek to Campbell County line (Day and Nelson 1929). Cheyenne, Wyoming, was built on the site of a large old colony (Day and Nelson 1929), where a ferret specimen was collected in 1877 (Coues 1877). Fragmentary records of prairie dog poisoning show that prairie dogs have been reduced by at least 75% since 1915 (Clark 1973). Clark et al. (1985) estimated that about 6,000 prairie dog colonies (ca 90,000 ha) still exist in Wyoming, but most are small and contain low densities of prairie dogs.

SASKATCHEWAN

Twenty-one specimens were located in one U.S. and four Canadian museums (Table 6). All of these specimens were collected in southern Saskatchewan with the exception of FMNH 8207, from Gleichen, Alberta (not mapped). Gleichen is several hundred kilometers out of present prairie dog range and is also disjunct from the next closest record of black-footed ferret in Saskatchewan. Because we have no other evidence to support ferret occurrence or recent prairie dog occurrence at that latitude at this time, we regard this record as spurious. It is possible the skin was picked up in fur shipments from another location and subsequently sold to FMNH.

Prairie dogs were not reported from Canada until 1927 (Soper 1938, 1944, 1946) and then only in the vicinity of Climax and Val Marie in extreme southwestern Saskatchewan. Ferret specimens were taken from 1924 to 1937 over a greater geographical area (Fig. 22). Prairie dogs may have been distributed at low densi-

ties or were expanding throughout southern Saskatchewan and Alberta at that time and were not recorded in biological surveys. Ground-dwelling rodents that might provide ferret habitat (with the exception of *Spermophilus richardsonii*) are absent in the area of ferret specimen distribution. Woodchuck (*Marmota monax*) and Franklin's ground squirrel (*S. franklinii*) are typically found at the eastern range of *Cynomys* in the continental U.S. and are found much farther north in Canada than the known distribution of prairie dogs (Hall 1981). Rather than imply an alternate habitat for the black-footed ferret in Canada, the distribution of ferret specimens more likely suggests the former range of *Cynomys*. The fossil history of *Cynomys* in Alberta goes back at least one million years. At Medicine Hat, *Cynomys* spp. has been found in Wisconsin-age deposits and *C. leucurus* has been identified in the Sangamonian and middle Wisconsinan faunas (Stalker et al. 1982). *Cynomys leucurus* has been at found at January Cave (late Wisconsin, J. Burns personal communication), and *C. ludovicianus* was recognized in the Hand Hills fauna (Storer 1975), although this identification has been questioned (J. Burns, personal communication). *Cynomys* has not been reported from any Pleistocene fauna in Saskatchewan. It is possible that intensive agriculture in the Prairie Provinces eliminated prairie dogs in many places before they could be recorded.

Prairie dogs totaled only 503 ha in 1971 and are currently found only near Val Marie (Kerwin and Scheelhaase 1971). Ferrets are considered extirpated in Canada by the Committee on the Status of Endangered Wildlife in Canada, 1978 (Thornback and Jenkins 1982).

Additional reports

Sixteen additional specimens are catalogued in museums with little or no identifying data (Table 6). Some of these may be the specimens that are "unknowns" from other locations. Some dates of acquisition can be guessed from catalogue numbers, but this is not reliable.

MCZ 14947, labeled as received in 1862, was collected by F. J. Thompson, who was the collector of record for Abilene, Taylor County, Texas, in 1882 (Coues 1882). This specimen was lost and may have been mislabeled in the MCZ collection. Five of the specimens in this group were collected for zoos. Along with the Canadian evidence, additional reports outside the range of *Cynomys* are specimen USNM 21965 listed from Licks River, Missouri, and a note by Ames (1874) listing "*P. nigripes*", with no evidence, in the fauna of Minnesota. However, these reports are far from potential range as determined by prairie dog distribution, and we conclude they are erroneously placed as originating in these locations. In the case of the Missouri account, for example, the specimen could have been taken on the Kansas plains and subsequently ascribed by the collector to his home location. No place name for Lick's River in Missouri could be found.

Summary

We list 412 specimens in Table 6. The current deposition is known for 310 of them. The largest number of state records (99) and extant specimens (50) are from South Dakota. Twenty-one specimens are noted from Canada. Only 6 specimens were collected outside of known prairie dog range, although the association of some of the Canadian specimens is uncertain. Of the 412 records, at least 103 (25%) were taken by federal predator and rodent control agents. The number taken by museum collectors is unknown but probably is also significant. At least 41 animals (10%) were captured alive and held by individuals or zoos.

Specimens collected by year are given in Figure 23 (n = 318). The highest collection figures date from the 1920s. This peak corresponds to the period in which the BSFW was entering numerous agreements with state extension services in the West to control prairie dogs and carrying out large-scale poisoning campaigns (Day and Nelson 1929, Linder et al. 1972, Hubbard and Schmitt 1984). Because ferrets never have been of economic value, many specimens that were taken up to this time probably were destroyed and never reported. Elsewhere, changing land use significantly reduced potential ferret habitat and contributed to ferret decline. In several eastern prairie states (Kansas, Nebraska, Oklahoma, Texas), 65% of all specimens collected date prior to 1910. The early demise of ferrets in these states is probably directly attrib-

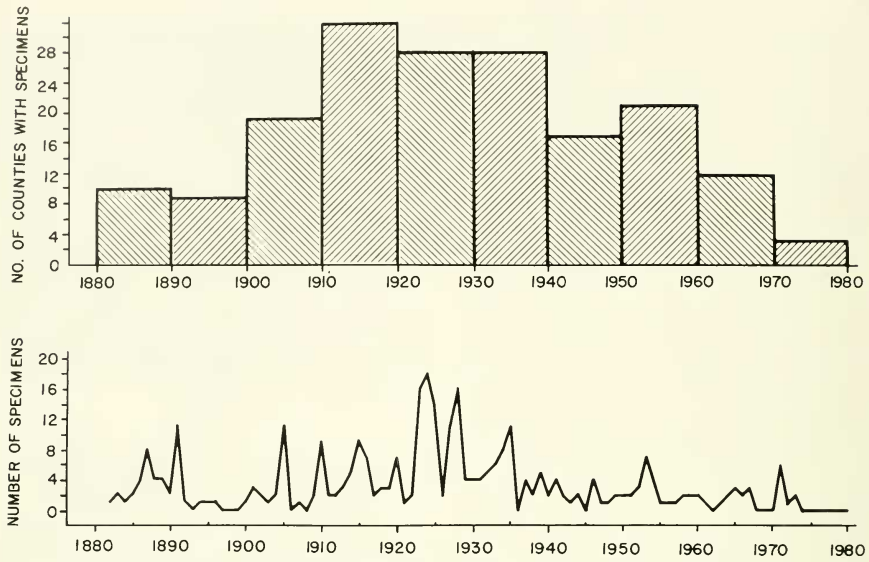

Fig. 23. Collection history of black-footed ferret specimens by county and by year (1880–1980).

utable to the expansion of population and cultivation into areas formerly occupied by prairie dogs.

In the 1950s disappearance of large areas occupied by prairie dogs stimulated interest in locating all possible remaining ferrets, but despite the more detailed accounting of sight and specimen reports (e.g., Cahalane 1954), specimen reports continued to decline, including the number of counties reporting specimens (Fig. 17). By the 1970s the number of known populations had dwindled to one, although in retrospect the population at Meeteetse was certainly extant as well as some individuals in Carter County, Montana. At the present time only the Meeteetse population is known.

Plotting locality records of ferrets with the ranges of three species of prairie dogs shows 83.0% are from *C. ludovicianus* range, 11.2% are from *C. leucurus* range, and 5.8% are from *C. gunnisoni* range. Our estimates of prairie dog abundance show that 41,900,000 ha of rangeland may have been occupied by all species of prairie dogs in the early part of the 1900s. Nelson (1919) estimated 40,469,500 ha. Current areas occupied in all the western states and provinces is unknown but is greatly reduced, perhaps by as much as 90%. Presently, ferrets are considered extirpated by U.S. and Canadian wildlife officials in Canada, Oklahoma, and Texas. Because of low prairie dog numbers, the likelihood of persistence of black-footed ferrets in Arizona, Kansas, Nebraska, and North Dakota is also poor. Ferrets may persist in the remaining states of its former range, but they are probably restricted to small, isolated populations.

Specimen collection by month is plotted in Figure 24. Seasonal changes in collection returns likely reflect phases in ferret life history and trapping efforts. Since trapping for most furbearers reaches its peak in midwinter, high returns are to be expected, particularly where ferrets are caught accidentally in sets for other animals. It is interesting to note that the peak month of collection is October, the time at which most newly independent young ferrets are dispersing (D. E. Biggins, personal communication cited in Forrest et al., *Black-footed ferret habitat*, 1985). The lowest specimen count occurs in June, when females with young remain for long periods underground.

Several authors have commented on the bias toward males in capture data for mus-

Fig. 24. Collection of black-footed ferret specimens (n = 234) by month based on all records (1851–1984).

telids (King 1975). The 200 ferret specimens of known sex in Table 3 (137 males and 67 females) show a sex ratio of 2.04M:1F. Since sex ratios at birth are 1:1 (Forrest et al., *Life history characteristics*, 1985), it seems likely that this collection bias is similar to trap biases seen for other mustelids, and is not a result of a skewed adult sex ratio. Trap biases in mustelids are a result of males having larger activity areas and longer movements (and therefore more encounters with traps or hazards) and being less trap-shy (King 1975, Powell 1979). Black-footed ferret males have larger activity areas (Biggins et al. 1985, Richardson et al. in preparation), which further supports this theory.

Morphometric Variation

Sexual Dimorphism

Adult females averaged 93% of male body length for both museum- and field-measured groups and were 68% of males in body weight. Skull length for females averages 93% of that of males based on CBL.

Five variables were chosen by stepwise maximizing of Wilks' lambda for cranial measurements as the best discriminators of sex: CBL, LC, POC, INB, and WM[1]. The results of the cranial discriminant analysis produced excellent discrimination between classes (Fig. 25). Coefficients for known specimens not

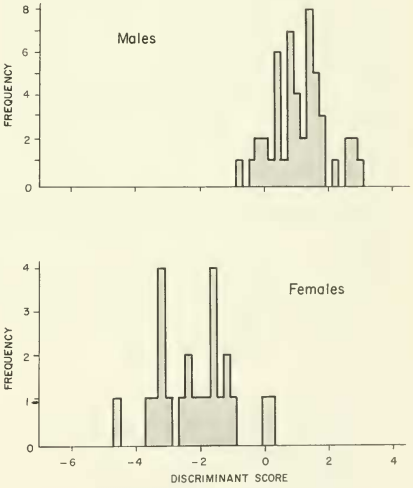

Fig. 25. Histogram of discriminant scores from a discriminant analysis between sexes of black-footed ferrets.

used in classification indicated that only 2.0% of males and 8.3% of females were misidentified on this basis, or that grouped cases were correctly classified 95.9% of the time. Because in many cases only mandibles may be found (particularly with fossil material), a second analysis using only mandibular variables

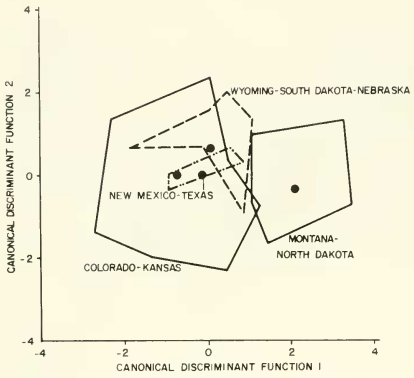

Fig. 26. Convex polygons containing the values for specimens of male *M. nigripes* from four localities (north-south) for their first two discriminant axes.

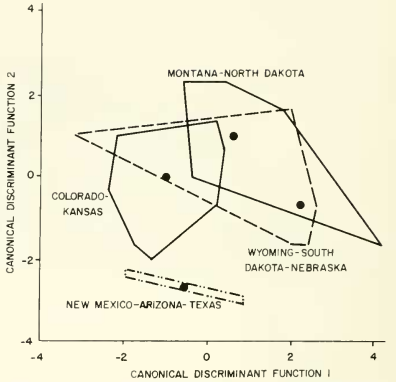

Fig. 27. Convex polygons containing the values for specimens of female *M. nigripes* from four localities (north-south) for their first two discriminant axes.

was made. Four mandibular variables (LJAW, DP_{3-4}, WM_1tal, and LM_1tr) were chosen by maximization of Wilks' lambda. Mandible measures are not as good as cranial measures as discriminators of sex, with 8.2% of males and 16.7% of females correctly classified (correct classification 89.4% of the time), but they can be used when crania are not available or cannot be classified.

To assign sex to crania and mandibles a decision is made based on the following equations derived from the discriminant analysis. For crania:

$$A = 19.954(CBL) + 14.129(INB) + 0.373(LC) + 24.790(POC) - 29.706(WM^1) - 877.213.$$

$$B = 18.936(CBL) + 11.681(INB) - 5.634(LC) + 23.099(POC) - 23.600(WM^1) - 758.034.$$

For mandibles:

$$A = 10.279(LJAW) + 13.849(DP_{3-4}) + 93.278(WM_1tal) + 65.965(LM_1tr) - 591.915.$$

$$B = 9.435(LJAW) + 11.416(DP_{3-4}) + 85.110(WM_1tal) + 63.392(LM_1tr) - 502.990.$$

If A > B, then the skull is from a male. If B > A, then the skull is from a female. If the absolute difference between A and B is greater than 2.80, then P > .05 that the skull has been correctly classified. If A = B or the difference between A and B is less than 0.50, then the probability of correct classification is less than 60%, and no determination can be made as to sex.

Geographic Variation

Linear discriminant analysis was performed on 29 cranial measurements of 50 males and 31 females from four geographic regions that correspond roughly to four latitudinal gradients arranged from north to south (Fig. 1). These regions were: Montana–North Dakota; Wyoming–South Dakota–Nebraska; Colorado–Kansas; New Mexico–Texas–Arizona.

The characters best separating males by region were: CBL, DP_{3-4}, LP^4, WM^1, and PBC-C. Characters best separating females by region were: CBL, DP_{3-4}, LP^4, WM^1, PBC-C, and WP^4pc. Discriminant scores and group centroids for the first two discriminant axes are shown in Figure 26 (males) and Figure 27 (females). There is evidence in this analysis of a north-south cline for both sexes, although overlap between clinal groups can be seen (Table 7). The extreme southern region (New Mexico-Arizona-Texas), overlaps the Colorado-Kansas region for males and appears separated on the axis for canonical function 2 for females. The southern group is included for completeness despite the obvious violation of multivariate assumptions caused by extremely small sample sizes. The present orientation of centroids is little affected by this region because of these small sample sizes. This partially explains high misclassification for both males and females in this group. Outcomes of discriminant classification in Table 7

TABLE 7. Discriminant classification of male and female black-footed ferrets from four localities showing number of members from each location correctly classified.

Actual group	Number of cases	Predicted group membership 1	2	3	4
FEMALES: 72.73% of "grouped" cases correctly classified					
1 (Montana, North Dakota)	8	6 (75.0%)	2 (25.0%)	0	0
2 (Wyoming, South Dakota, Nebraska)	7	1 (14.3%)	5 (71.4%)	1 (14.3%)	0
3 (Colorado, Kansas)	16	3 (18.8%)	0	11 (68.8%)	2 (12.5%)
4 (New Mexico, Arizona, Texas)	2	0	0	0	2 (100.0%)
MALES: 56.86% of "grouped" cases correctly classified					
1 (Montana, North Dakota)	8	7 (87.5%)	1 (12.5%)	0	0
2 (Wyoming, South Dakota)	8	1 (12.5%)	4 (50.0%)	1 (12.5%)	2 (25.0%)
3 (Colorado, Kansas)	31	2 (6.5%)	5 (16.1%)	17 (54.8%)	7 (22.6%)
4 (New Mexico, Arizona, Texas)	4	0	2 (50.0%)	1 (25.0%)	1 (25.0%)

show higher overlap of nearer clinal groups and little or no overlap as clinal groups become farther apart.

Further analysis reveals that the source of this variation is primarily found in differences in size from north to south and not in changes in relationships of variables to each other. This is indicated by Figure 28 for CBL, which shows significantly larger measurements between northern and southern groups for both males and females (males: $F = 4.3$, 44 df, $P = .04$; females: $F = 5.1$, 25 df, $P = .03$). ANOVA between the two northernmost and two southernmost groups showed significant differences in 17 of the 29 variables tested, with larger measurements from the northern group.

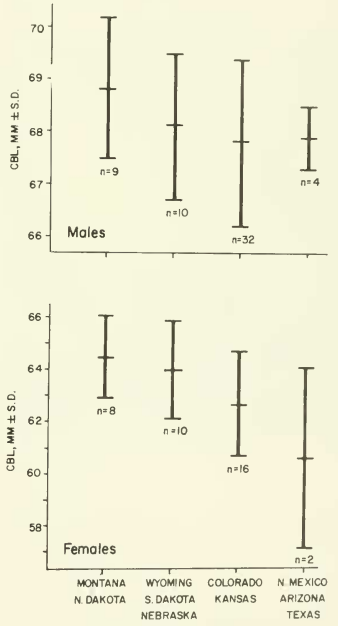

Fig. 28. Latitudinal differences in CBL for male and female black-footed ferrets showing a north-south cline in size.

Prey Species Variation

Discriminant analysis was also used to test for differences between ferret specimens associated with different prairie dog species. The subgenus *Leucocrossuromys* includes *C. gunnisoni*, *C. leucurus*, and *C. parvidens*. The subgenus *Cynomys* includes *C. ludovicianus* and *C. mexicanus* (Mexican prairie dog). *Leucocrossuromys* is considered more like ancestral *Spermophilus* than *Cynomys*; shows a less interactive social organization, organized around clans; and has a short white-tipped tail, a less massive skull, and smaller and less expanded cheek teeth (Clark 1973a). Subgenus *Cynomys* has a longer black-tipped tail, distinct reddish-cinnamon pelage in summer, and a more complex social organization than *Leucocrossuromys*, organized around coteries (King 1955, Hoogland 1981). The current distributions of the two subgenera show an elevational and longitudinal cline, since the white-tailed species is found at higher elevations along the western portion of prairie dog range. Since the subgenera occur at dif-

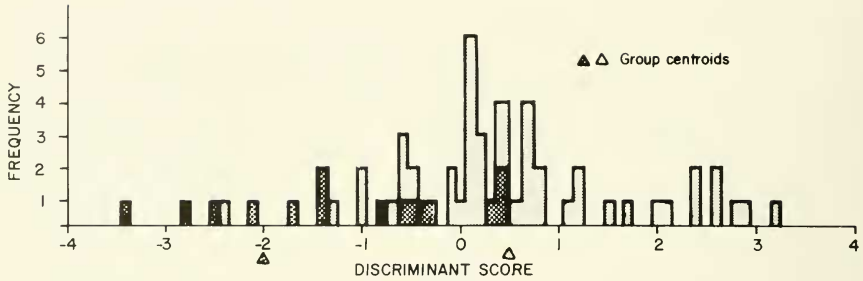

Fig. 29. Histogram of discriminant scores from a discriminant analysis between *M. nigripes* specimens taken from black-tailed prairie dog range (dark shading) and white-tailed prairie dog range (light shading).

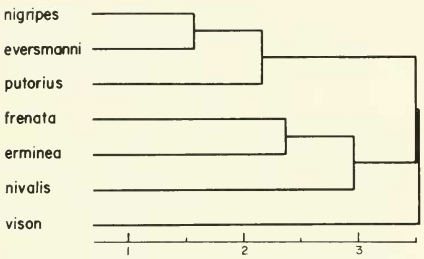

Fig. 30. Single linkage dendrogram using generalized distances between species centroids based on a consensus of *Mustela* males and females (after Youngman 1982).

ferent densities, have different behavior patterns, and are geographically separated, it might be expected that ferret differentiation may have evolved with each subgenus of prairie dog, which could be reflected in morphological differences. For example, prairie dogs show similar external sizes and dimensions among species (Hall 1981) but may differ along similar latitudinal gradients. Size differences could be reflected in the size of burrow openings used and weight of the animal, which could in turn affect the size or conformation of ferrets found with them.

Because of north-south clinal variation and sexual variation among ferrets, comparisons were made only between male ferrets from the range of black-tailed prairie dog (n=50) and ferrets from the range of white-tailed prairie dog (n=15) subgenera from the two regions closest to the geographic center of ferret range (Wyoming-South Dakota-Nebraska and Colorado-Kansas). Although six variables (1NB, WBC, WM_1tr, LC-M^1, WC, and WM_1tal) were chosen by stepwise maximizing of Wilk's lambda, which discriminated between white-tailed and black-tailed prey groups, only 53.3% of the white-tailed group were placed correctly in that category, indicating a high degree of overlap between groups (Fig. 29). This analysis suggests that no morphometric variation in black-footed ferrets occurs based on the species of prairie dog they are found to associate with. However, other differences may exist that involve ecological or behavioral characteristics that could taxonomically separate these groups but are not reflected in morphometric analyses.

Ferrets and Their Relatives

The genus *Mustela* includes weasels (subgenus *Mustela*), mink (subgenera *Lutreola* and *Vison*, see Youngman 1982), ferrets and polecats, (subgenus *Putorius*; European workers often use *Putorius* as a generic name), and South American weasels (subgenus *Grammogale*). "Ferret" and "polecat" are interchangeable common names, though polecat is generally used for the Old World species. Based on single linkage dendrograms derived from morphometric variables, Youngman (1982) suggested that the polecats *M. putorius*, *M. eversmanni*, and *M. nigripes*, form a natural group distinct from the weasels and *M. vison*. Figure 30 shows the phylogenetic relationships of some of the species in this group. These highly efficient small carnivores range in size from the tiny least weasel (*M. nivalis rixosa*, wt 38–63 gm), the smallest living carnivore, to the Siberian or steppe polecat (*M. eversmanni*, wt to 2050

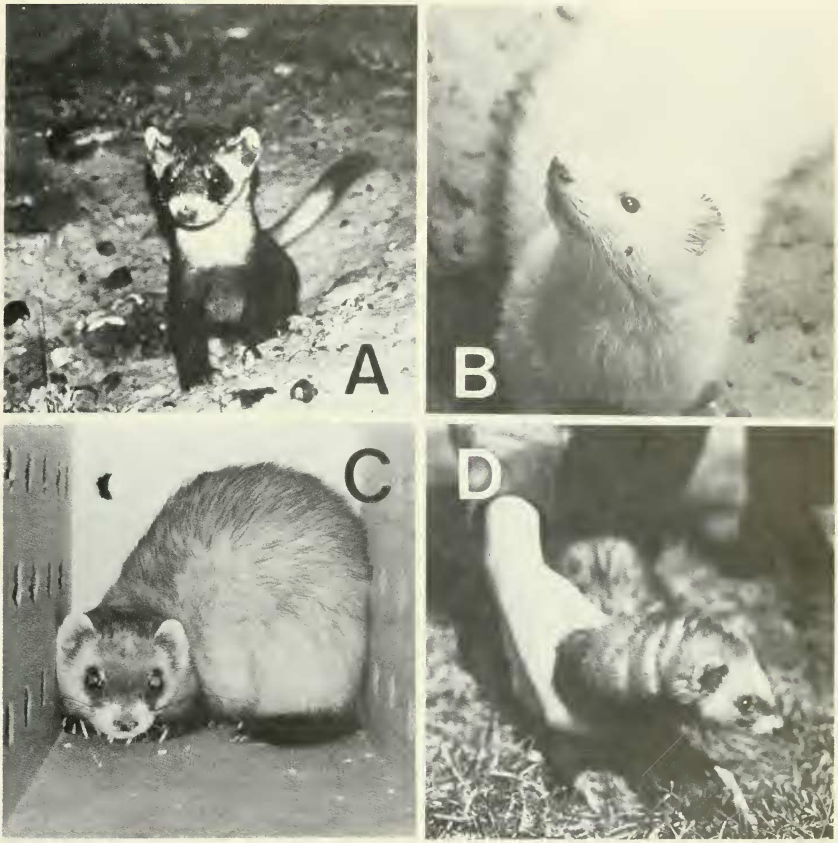

Fig. 31. Photographs of *M. nigripes* (A), *M. vison* (B), *M. eversmanni* (C), and *M. putorius furo* (D).

gm). All of them have a long lithe body, short legs, a long low braincase, and short powerful jaws equipped with elongated bladelike carnassials (P^4, M_1), sharp canines, and three premolars in each jaw half (two in the lower jaw of the South American weasel, *M. africana*). Primarily Holarctic in distribution, weasels and ferrets are terrestrial and mink semiaquatic. About 15 extant species are recognized.

Of these, only four, *M. nigripes*, *M. eversmanni*, *M. putorius*, and *M. vison*, concern us here. Table 8 compares the four species and Figure 31 illustrates them. Although mink and ferrets differ markedly from each other in appearance, their skulls and teeth are similar and can be confused. Table 9 shows some differences between them.

The domestic ferret (*M. putorius furo*) was bred in captivity as early as the fourth century B.C. for use in controlling rodents and driving rabbits from their burrows (Nowak and Paradiso 1983). It is also kept as a pet. Leonardo da Vinci's famous painting "The Lady with a Weasel" actually depicts the domestic ferret (Kowalski 1976). Its distribution is now worldwide in captivity. Coloration is generally pale yellow or whitish (often albino) with no black or dark markings. Escaped domestic ferrets have been mistaken for black-footed

TABLE 8. Comparisons between *Mustela nigripes*, *M. eversmanni*, *M. putorius*, and *M. vison*.

	M. nigripes	*M. eversmanni*	*M. putorius*	*M. vison*
Geologic range	Early late Pleistocene–Recent	Mid-Pleistocene–Recent	Mid-Pleistocene–Recent	Mid-Pleistocene–Recent
Geographic range	Formerly S Canada, Great Plains to NW Texas, SW U.S.	Steppes of Eurasia, S to central Asia, NE China	Europe E to Ural Mountains	North America except arid areas. Introduced in Europe
Habitat	Prairies, mountain basins, semiarid grasslands	Open grasslands	Open forests, meadows, clearings	Along streams, marshes
External characters	Upper parts yellowish buff. Feet black, black mask across eyes, tail tip black	Yellowish to pale brown. Dark feet, dark mask across eyes, terminal 1/3 tail dark	Dark brown to black, belly dark, silvery between eyes and ears, tail entirely dark	Rich dark brown, white chin patch, tail slightly bushy
Size	♂ TL 490–615, T 107–148, Wt 915–1125 g. ♀ TL 479–565, T 109–141, Wt 645–850 g.	♂ TL 450–740, T 80–183, Wt to 2050 g. ♀ TL 360–700, T 70–180, Wt to 1350 g.	♂ TL 465–650, T 115–190, Wt 500–1500 g. ♀ TL 375–465, T 85–125, Wt to 1360 g.	♂ TL 510–570, T 180–230, Wt 680–1360 g. ♀ TL 430–560, T 130–200, Wt 565–1089 g.
Food	*Cynomys*, rodents, lagomorphs	Pikas, susliks, voles, hamsters, marmots	Mice, toads and frogs, birds	Aquatic mammals, birds, frogs, fish, crayfish
Habits	Mostly nocturnal, solitary. Closely associated with *Cynomys*	Nocturnal. Live in rodent burrows. Avoids contacts with man	Nocturnal, solitary. Often found around barns, dwellings	Nocturnal, solitary. Den along streams
Reproduction	Gestation period 42–45 days. 3–5 young born May–June	Gestation period 38–41 days. 4–9 young born April–May	Gestation period 40–43 days. 4–6 young born May–June	Gestation period 40–91 days. Short delayed implantation. 2–6 young born April–May
Remarks	Endangered species. Closely related to *M. eversmanni*.	Striking resemblance to *M. nigripes*. Hunting of *M. e.* prohibited in Siberia	Fur valuable (fitch). Subspecies *M.p. furo* domesticated, used in hunting and as pets	Fur valuable. Raised on fur farms

TABLE 9. Comparisons between *Mustela nigripes/eversmanni* and *M. vison* (after Anderson 1977).

Variant	*M. nigripes/eversmanni*	*M. vison*
Palate	Wide between canines	Narrow between canines
Basiocciput	Narrow	Wide
Basicranium	Well-developed tube extending from foramen ovale to anterior margin of auditory bulla	No tube. Area between foramen ovale and auditory bulla flat
Auditory bullae	More inflated	Less inflated
Auditory meatus	External opening large	External opening small
Mastoid bullae	Inflated	Not inflated
Infraorbital foramen	Small	Large
Jugal	Wide	Narrow
Frontals	Rounded	Flattened
Canines, upper and lower	Relatively large	Relatively small
P^3	Short, broad	Long, narrow
P^4	Relatively short protocone	Relatively long protocone
M^1	Inner lobe not expanded	Inner lobe expanded
Mandible	Relatively short and thick	Relatively long and slender
Inferior margin of jaw at angle	Broad, flattened	Narrower, less flattened
Lower premolars	Relatively short, broad	Relatively long, slender
M_1	Metaconid absent, talonid narrow	Incipient metaconid, talonid broad
M_2	Relatively small	Relatively large

ferrets (Choate et al. 1982), but they are entirely different in appearance (Fig. 31).

Polecats probably arose in Europe in the Villafranchian (3–4 mil yrs B.P.). The earliest known species, Stromers polecat (*M. stromeri*), ranged from the late Villafranchian to the middle Pleistocene, when it was replaced by the modern species. Though smaller in size, Stromer's polecat was closely allied to the European polecat (*M. putorius*) and was probably ancestral to both the European polecat and the steppe polecat (*M. eversmanni*). These two polecats have been considered conspecific by some workers, but studies by Russian mammalogists (Stroganov 1962) have shown them to be distinct, well-defined species that differ in size, coloration, and habitat. Although their ranges overlap in Hungary, Romania, and southern European Russia, they are nowhere truly sympatric, being separated by different habitat preferences (Corbet 1966). Hybrids occur only under exceptional circumstances. Unlike *M. nigripes*, the steppe polecat is not closely associated with any one species of rodent and feeds on susliks (*Spermophilus* spp.), marmots, hamsters and voles; in winter, pikas (*Ochotona* spp.) are a major food source in some areas. Rodent burrows, especially those of susliks, are often expropriated by polecats for shelter and dens, though they may dig their own. *Mustela eversmanni* is valued as an exterminator of rodents and for its fur, which is, however, of lower quality than that of *M. putorius*. Although *M. eversmanni* is not considered to be endangered, hunting the animal in Siberia is prohibited.

Mustela eversmanni and *M. nigripes* are closely related, and their possible conspecificity has been noted by several workers (see Youngman 1982 for references). Although their size and coloration are similar, and analysis shows only slight differences in cranial and dental measurements (Figs. 20, 21, 22), Anderson (1977) considers them separate entities.

That the two species are closely related cannot be doubted, but until detailed comparative and statistical studies are made on the large collections of *Mustela eversmanni* in Soviet institutions, these data are compared with the information already compiled on *Mustela nigripes*, and behavioral and chromosomal studies are undertaken on both species, I regard them as distinct.

Detailed studies are still lacking for *M. eversmanni*, and so far there have not been any studies on genetic variation between the two species, so the question of *M. eversmanni* and *M. nigripes* conspecificity remains unresolved.

Another taxonomic problem in the ferrets is the recognition of subspecies. No subspecies of *M. nigripes* have ever been named, and our studies do not show any taxonomically significant geographic variations between samples. Two or perhaps three subspecies of *M. putorious* are recognized based on slight differences in size and color. Seventeen subspecies of *M. eversmanni* have been described, eight of them from Siberia. Strogonov (1962:370) said, "The Siberian polecat shows more geographical variation than the European polecat, this being manifested in changes in fur structure and in dimensions of body, skull and claws." Whether all of these subspecies are valid or merely represent oversplitting is unknown. Of the three species of polecats, *M. eversmanni* has by far the largest geographic range, extending from Hungary to far eastern Asia across the broad band of steppes, forest steppes, and semideserts between 50° and 60° N latitude.

The historic range of *M. nigripes* included the Great Plains and mountain valleys. This was a relatively homogeneous environment without major geographic barriers. However, Endler (1977) points out that there is no evidence that allopatry is necessary for differentiation. Gradation within a continuous range (parapatry) is very common, as is pointed out by the north-south differentiation demonstrated for *M. nigripes* in this paper. Additional specimens from the northern and southern extremes of the range would probably demonstrate more strongly this clinal variation. Whether geographic isolation, for example, in South Park, Colorado (USNM 247073), would eventually have resulted in distinct subspecies will, of course, never be known.

Ferrets entered North America from Siberia, spread across Beringia, and then advanced southward through icefree corridors to the Great Plains. Kalela (cited in Kurtén 1957) noted that between 1880 and 1940, *M. putorius* extended its range in Finland from the Karelian Isthmus north to central Os-

trobothnia and west to the Gulf of Bothnia at a rate of 7.5 km annually or 750 km/century. This rate is probably applicable for ferrets spreading across Siberia into the New World in the Pleistocene, when conditions were favorable.

DISCUSSION

Our evidence supports the contention of others (e.g., Linder et al. 1972, Hubbard and Schmitt 1984) that black-footed ferrets were probably common historically. We have located physical remains or verified reports of ferrets from 128 of 513 counties (25%) within the historic range of *Cynomys*. A conservative estimate is that 41,000,000 ha of western grasslands were occupied by prairie dogs in the early part of this century. Using the Forrest et al. (*Life history characteristics*, 1985) population density estimate of one ferret per 40–60 ha, habitat may have been available in the past to support as many as 500,000–1,000,000 black-footed ferrets, if this habitat were fully occupied by ferrets.

Although the Canadian specimens cast some doubt on the nearly obligate association between ferrets and prairie dogs, it is almost certain that alternate habitats do not provide adequate resources to support ferrets in the long term. If ferrets were living in habitats other than prairie dog colonies in Canada, then they should still be extant there; yet the last specimen was taken in 1937, about the time remnant prairie dogs in Canada were being eliminated by expansion of agriculture.

Geographic variation in a species has implications for any recovery program involving reintroduction of animals into areas where they have been extirpated. It would not be prudent to attempt such reintroductions using animals that differ greatly from those that originally occurred in the reintroduction area. However, with black-footed ferrets there seems to be little habitat-related variation, and reintroductions should prove successful in any geographic area with any prairie dog species serving as prey, provided sufficient habitat still remains to support the ferrets and their prey. With regard to clinal or other geographic variation, our analyses suggest that a case can be made for morphometric variation within this species, although the usefulness of this argument seems limited to the case where numerous populations are competing for protection (Schonewald-Cox et al. 1985), which is not the case for this species.

The possibility that the steppe ferret and the black-footed ferret are representatives of a single holarctic species exploiting similar ecological niches in the New World and Old has been suggested. This in no way diminishes the unique position the black-footed ferret holds in the prairie ecosystems of this continent. It does suggest that options that might draw on *M. eversmanni* to assist in recovery efforts for the endangered *M. nigripes* should be further explored.

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